THE GROWING PLANT

by the same author

*

in conjunction with Dr. M. C. Rayner
PROBLEMS IN TREE NUTRITION

THE GROWING PLANT

by

W. NEILSON-JONES

FABER AND FABER LIMITED
24 Russell Square
London

First published in mcmxlviii
by Faber and Faber Limited
24 Russell Square London W.C.1
Printed in Great Britain by
Latimer Trend & Co Ltd Plymouth

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ILLUSTRATIONS

ACKNOWLEDGEMENTS

Grateful acknowledgements are due for permission to reproduce many of the illustrations to this book. Plate 2 comprises two original photographs by Mr. Stephen H. Willard of Palm Springs, California; Plate 4 is from Dr. F. Y. Henderson's *Timber* (Crosby, Lockwood & Co.); Plates 5 and 7 are from papers by Dr. M. A. H. Tincker in the *Jour. Roy. Hort. Soc. 63*, 210 and *54*, 354 respectively; Plate 6 is from a photograph supplied by Prof. F. G. Gregory, illustrating a lecture by Prof. V. H. Blackman to the Roy. Hort. Soc. and printed in the Society's Journal; Plates 8 and 9 are from Dr. Rayner's *Trees and Toadstools* and *Problems in Tree Nutritution* respectively (Faber and Faber). Among the text-figures, Figs. 3, 4 and 5 are from papers by Dr. H. Godwin, the first in the *New Phytologist*, the two last in *Trans. Roy. Soc.*; Fig. 19 is from Dr. K. M. Smith's *Plant Viruses* (Methuen & Co.); Figs. 32 and 33 are from *Genetics of Garden Plants* by M. B. Crane and W. J. C. Lawrence (Macmillan & Co.). I have also to thank Messrs. Methuen & Co. for permission to reproduce Figs. 9–13 and 16–18 from my own *Plant Chimaeras and Graft Hybrids*.

I must express special gratitude to my wife for the many fruitful criticisms and suggestions made in the course of reading the proofs.

PREFACE

The preface of a book is expected to provide some indication of the author's purpose in writing it and serve as a guide to the potential purchaser in respect of the character of the contents.

The general public hear tales of the long periods seeds can survive storage without loss of vitality, but often have personal experience of the poor germination of flower seeds kept even for one year. Should they wish to plant an orchard with the variety of apple known as 'Cox's Orange Pippin', they are told that they must interplant with another variety to ensure a plentiful fruit crop. They have heard that penicillin is derived from a mould; that flowers can be obtained out of season by appropriate treatments; that some plants require more prolonged daylight than others in order to produce flowers. Many would be glad to know the truth about these and kindred matters, but either they may not find any reference to the subjects in which they are interested in the botanical text-books they consult or they are discouraged by the wealth of detail and technical terms they encounter in their search for enlightenment.

One object of the present volume is to provide the non-botanist with information about a number of aspects of plant life that in the author's experience provoke general interest. On the other hand, although many of the topics included are of considerable theoretical interest and practical importance, they find small space in many of the current text-books. It is believed that most students of botany would find the subject more stimulating if their academic studies were occasionally leavened

by references to the impact of the results of botanical research on the everyday world.

It will be understood, therefore, that this is in no sense a botanical text-book; nor does it attempt to give a balanced view of botanical science as a whole or of any individual branch of botany. Consideration of the isolated problems included in this volume will certainly not make the reader into a botanist, but it may perhaps so quicken his interest in plant life that, if not already a botanist, he may aspire to become one. The student of botany may find it convenient to have collected together certain matters usually treated only in advanced texts or in scientific journals that, at least to the elementary student or lay reader, may not be easily accessible.

At the end of each chapter is a short list of reference books relating in the main to the matters dealt with therein. From the many such references that might have been included, these have been selected largely because they are not too technical for the general reader to follow and as likely to be available in local libraries.

W. NEILSON-JONES

Bedford College,
University of London, 1947.

Chapter 1

THE PLANT AS INFORMANT

Plants, mute witnesses though they may be, convey a great deal of information about a variety of things both past and present. They have even been accredited with prescience. Apart from such absurdities as the basing of predictions on the behaviour of tea leaves, regarded seriously by no one, many people, quite rational in other respects, tell you it will be a hard winter because the holly is loaded with berries. Such forecast is based, presumably, on a vague conception that the trees, anticipating a severe winter, produce an abundance of berries under the direction of Providence for the sustenance of birds and other animals that may be short of food. In actual fact, of course, abundance of berries betokens a favourable past season rather than any relation with weather to come, except in so far as there may be some correlation in the kind of seasons that follow one another in different years.

Since botanists might be expected to be at an advantage in securing any benefits to be derived from plant prognostication, it is with a sense of personal regret that the writer must admit that claims to foreknowledge on the part of plants are without justification. On the other hand, forecasts of considerable practical importance have been based on data derived from plants; an instance in which the design of a large engineering project was based on a preliminary botanical investigation is referred to later in this chapter (p. 26).

Plants as soil indicators[1]

In respect to their immediate surroundings plants can tell one a good deal. Often the character of a soil may be inferred from the kinds of plants growing in it, although precise and detailed information about this might call for the taking of soil samples and subjection of these to soil analysis. Such a survey based on the plant species present is often of considerable value; it enables the main characteristics of large areas to be summed up rapidly even when the vegetational covering or some other cause makes the soil itself difficult of access.

To take an obvious and elementary example, the presence of Rock Rose (*Helianthemum Chamaecistus*), Traveller's Joy (*Clematis Vitalba*), or Horse-shoe Vetch (*Hippocrepis comosa*) makes it almost certain that chalk or limestone is near the surface, so giving rise to a calcareous soil; the occurrence of Foxglove (*Digitalis purpurea*), or Ling (*Calluna vulgaris*), on the other hand, is a sign that the upper layers of soil almost certainly have an acid reaction and are therefore not calcareous.

Deductions of this kind must be made with due care and knowledge because certain species commonly associated with, let us say, chalk downs are not confined to such locations, but are found there because they require good drainage or prefer a neutral or alkaline reaction; they may be found on any soils supplying these conditions apart from the content of calcareous material. Thus the frequent occurrence on chalk downs of the grass commonly called Yorkshire Fog (*Holcus lanatus*) does not in itself suffice to make this plant an 'indicator' for calcareous soils, since experience shows it to have wide tolerance towards soils differing considerably in calcareous content; on the other hand, Horse-shoe Vetch (*Hippocrepis comosa*) is almost exclusively restricted to calcareous soils and can therefore be regarded as a useful indicator. Incidentally, the abundance or even dominance of a particular kind of plant in the vegetation is of little significance in this connection; but species of rare or local occurrence, as for example the Pasque Flower (*Anemone Pul-*

[1] Sampson, A. W. 'Plant Indicators.' *Bot. Rev.* 5, 155, 1939.

satilla), are thoroughly reliable as indicators of calcareous soil.

Calcareous soils, i.e. those containing a high proportion of chalk or limestone particles, owe their alkaline reaction to the calcium carbonate of which these rocks mainly consist. It should be noted, however, that alkalinity may be conferred by salts of elements other than calcium as in some of the 'alkali soils' of arid regions in North America and elsewhere in which sodium carbonate is mainly responsible for the alkaline reaction. Alkalinity from a similar cause may also arise from artificial irrigation in desert regions. In Britain, however, the occurrence of soil alkalinity is almost always associated with the presence of calcium carbonate, i.e. with calcareous soils.

Plant species consistently absent from calcareous soils are usually those intolerant of the alkaline reaction accompanying the presence of much calcium carbonate, the main constituent of chalk and limestone and by far the most abundant calcium compound in soils. They are sometimes known as *calcifuge*—chalk-fleeing—species in contrast to *calcicolous* or chalk-loving plants. Since the determining factor is usually an alkaline reaction or the reverse, members of the former group might be better described as *basifuge* than as calcifuge. Many plants other than those belonging to the flowering plants may also be useful indicators of certain soil characteristics; for instance, with few exceptions the Bog Mosses (*Sphagnum* spp.) grow only in bogs formed by drainage water from highly acid and non-calcareous sources.

The distinction between calcareous and non-calcareous soils is an obvious and simple one in which the verdict of certain plants may be accepted with confidence. The presence of species such as the Sorrels (*Rumex acetosa* and *R. acetosella*), Bent Grass (*Agrostis vulgaris*), or Spurry (*Spergula arvensis*) usually indicates that the soil is acid in reaction; but just as 'chalk-loving' species may be those tolerating rather than demanding a high content of chalk or limestone with the alkaline reaction that is associated with it, so these characteristic plants of acid soils are often species that tolerate poor soils, acid or otherwise, and are therefore able to compete successfully with other species less tolerant of these conditions.

More rarely, individual species or varieties are largely confined to soils containing an unusually large amount of some particular element, serving therefore as indicators for the presence of this element. A well-known instance is the presence of *Viola calaminaria* and *Thlaspi calaminare*, commonly regarded as varieties of the Pansy (*Viola tricolor*) and Penny Cress (*Thlaspi alpestre*) respectively, on the workings of old zinc mines. The specific names '*calaminaria*' and '*calaminare*' are given because the naturally occurring zinc carbonate is called *calamine*.

As further examples may be cited certain members of the Pea family, for example *Astragalus pattersonii* and *A. confertiflorus*, and a member of the Composite family rejoicing in the name of *Xylorrhiza venusta*, which occur in Colorado, Utah, and elsewhere in North America, where they are confined to soils derived from rocks containing compounds of the rare element selenium, a member of the sulphur group, and so serve as 'indicators' of this metal.[1] [2] The amount of poisonous selenium compounds may be so high in plants growing in these areas as to preclude the grazing of cattle on the local pastures (see p. 125).

On occasion, the expected preferences of an indicator plant may fail to be exhibited, especially if the soil constituents are unusual. Thus Bracken (*Pteridium aquilinum*), a characteristic plant of acid soils with low calcium content, may sometimes appear on a soil rich in calcium carbonate provided other soluble salts are present in minimal quantities. Such exceptions do not impugn the reliability of deductions about soil conditions, but emphasize that the more thoroughly known are the soil preferences of plant species the more reliable are those deductions likely to be.

The composition of the surface vegetation, besides giving information about the chemical nature of the soil, also indicates its water-holding and water-yielding capacities. Thus, it is a commonplace that the presence of Bracken (*Pteridium aquilinum*),

[1] Trelease, S. F. and Trelease, H. M. 'Selenium as a stimulating and possibly essential element for indicator plants.' *Am. Jour. Bot.* 25, 372, 1938.

[2] Beath, O. A. 'Toxic vegetation growing on the Salt Wash Sandstone member of the Morrison Formation.' *Am. Jour. Bot.*, 30, 698, 1943.

Harebell (*Campanula rotundifolia*), etc., indicates a dry sandy situation, just as Bog Myrtle (*Myrica Gale*), Cross-leaved Heather (*Erica Tetralix*) and the Heath Gentian (*Gentiana pneumonanthe*) are characteristic of marshy ground, whilst many of the Willows are limited to river banks, although some, e.g. the Dwarf Willow (*Salix repens*), grow on heaths. The information given by Willows that a stream is nearby is somewhat of the kind given by people when they tell you it is a fine morning; the fact is usually patent without requiring to be pointed out. On the other hand, in a desert climate, a difference in the vegetation marking the course of an underground stream (Pl. 1, 2B; facing p. 20, 21) or the presence of springs (Pl. 2A; facing p. 21) in an otherwise apparently uniform desert landscape may provide information of practical value where water is scarce. To a thirsty distant cluster the desert, no sight could be more welcome than a traveller in of palms with their promise of a source of water relatively near the surface.

In short, the kind of plants that occur in any natural area provides those familiar with their habits with a good deal of reliable general information as to the nature of the soil, water supply, and so on; the amount of such information derived from a brief survey of the vegetation may indeed be far greater than could be obtained by other means in a longer time at the expenditure of much labour.

Plants as indicators of atmospheric and climatic conditions

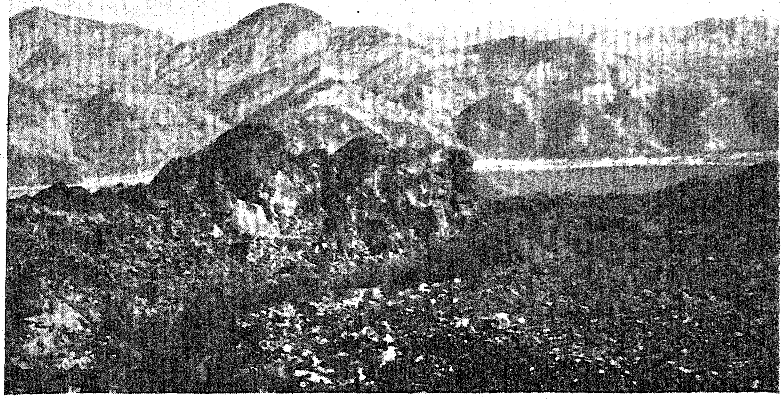
Not only are plants responsive to the chemical constitution and physical characters of the soils in which they grow, but they are extremely sensitive to certain impurities in the air surrounding them. Everyone is aware of the blighting effect produced on vegetation in general by the smoke of great cities in which manufacturing processes are carried out on an extensive scale, effects that may extend for many miles into the surrounding countryside, due not only to the deposit of the solid products of combustion on the leaves and shoots but also to the presence of deleterious gases. What is not always realized is the extreme

sensitiveness with which certain kinds of plants react to the less obvious gaseous by-products of urban life. Conifers and evergreens generally are intolerant of town life, while lichens are so sensitive to traces of industrial pollution in the atmosphere that even large open spaces within a city, such as Regent's Park or Hampstead Heath in London, are almost devoid of them; only well outside the town atmosphere are lichens represented by any considerable number of species or colonies.

Some species of flowering plants are highly sensitive to particular chemical substances that may occur as impurities in the air, so sensitive that they may be used as indicators for traces of the substances in question in preference to chemical methods of detection, as are canaries for the detection of carbon monoxide in coal mines. Young tomato or potato seedlings, for example, are highly sensitive to coal gas, in particular to the constituent of it known as ethylene, so that the reaction of these plants may be used to detect small leaks of coal gas that produce contamination of a few parts in a million.[1] The testimony of tomato seedlings has been accepted in the New York Law Courts as evidence of an escape of gas from the mains in an action brought by a firm of growers calling upon the gas company to repair their pipes. The gas company denied responsibility for damaged nursery stock and maintained there was no leakage of gas, but the behaviour of tomato plants as observed by experts from a botanical research station in the neighbourhood proved beyond doubt that such leakage was taking place and the growers won their case!

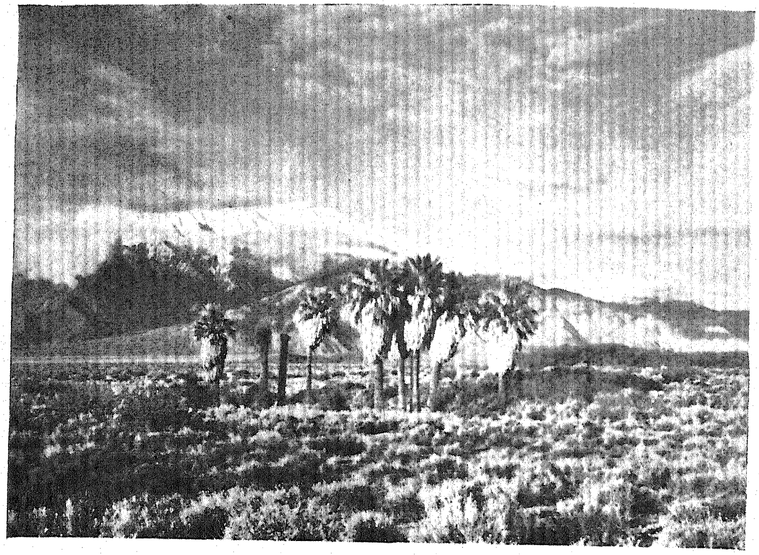
The response shown by plants of tomato to traces of ethylene and therefore of coal gas consists of a characteristic downward bending and curling of the leaves; it comes about in a few hours and besides being more sensitive than chemical methods of detection is more speedy and less laborious; all that is needed is a few young tomato plants in pots placed where the escape of gas is suspected and a botanical expert to record their behaviour (Pl. 3; facing p. 28).

[1] Crocker, William. 'A delicate method of detecting illuminating gas in a greenhouse.' *Flor. Exch.* *70*, 15, 54, 1929. (Also in *Boyce Thompson Inst., Prof. Pap.*, *1*, 81, 1929.)



1A. Colorado Desert, southern California. View down Andreas Cañon with open desert beyond. A small stream of running water occurs in the cañon, disappearing below ground on reaching the low desert plain. The position of the stream is marked by the occurrence of Cotton-woods (*Populus fremontii*), the underground water in the desert plain beyond the mouth of the cañon by a cluster of palms (*Washingtonia filifera*), recognizable by their darker and denser foliage.

1B. Colorado Desert, southern California. Dry stream-bed on the Vandervanter Trail in the foothills of San Jacinto Mountain. The presence of underground water is indicated by the presence of plane trees ('Western Sycamore'—*Platanus racemosa*).



2A. Colorado Desert, southern California. 'Seven Palms', an oasis having a spring of alkaline water. San Jacinto mountain in the background is seven or eight miles distant, rising to a height of 11,000 feet.

2B. Colorado Desert, southern California. Palm Cañon near Palm Springs, the presence of palms on the floor of the cañon indicating the presence of underground water. *Washingtonia filifera*, the palm shown in these photographs, has the habit of retaining its old leaves which form a wide investment round the trunk; the palms in 2A have lost the lower part of this natural investment from burning, Seven Palms being often visited by campers.

Plants may furnish also a useful indication of the climatic conditions of the localities in which they grow. Thus, persistence of tender species is a tribute to the general mildness of the climate and its freedom from severe frosts in winter; abundance of ferns and mosses, as in many parts of western and south-western England, reflects a humid climate with frequent precipitation; trees in an open unsheltered position showing a one-sided development betoken the occurrence of strong winds, the less-developed side of the trees facing the direction from which the prevailing winds blow; and so on.

Plants as indicators of time and direction

Many flowers open only in full sunshine and so inform one, somewhat superfluously, that the sun is shining. Of more interest is the fact that certain plants open and close their flowers at fairly regular hours. Flowers of some, such as those of the Morning Glory (*Ipomoea purpurea*) and wild Rose, open at dawn; those of most Tulips open between nine and ten o'clock in the morning; those of Honeysuckle (*Lonicera* sp.) about 6 p.m., and of certain species of Catchfly and Tobacco (*Silene longiflora* and *Nicotiana affinis*) between eight and nine in the evening. It was upon such behaviour that Linnaeus devised his 'floral clock', at one time a popular botanical curiosity in public gardens, in which plants were grouped in a series of beds arranged in a circle to present the hours on a clock face according to the hours at which their flowers were open or closed.

That is the theory on which the construction of such a clock is based; unfortunately, its practical realization proves to be far less simple than is suggested in the last paragraph. To begin with, there is the obvious difficulty that most plants have a comparatively short flowering season, blooming at a time of year that varies with the kind of plant. Each of the beds representing an hour will thus need to contain several different plant species if the clock is to function for more than a very brief period. Then there is the further complication that many plants with a more prolonged flowering period open and close their

flowers at different hours at the beginning and end of their flowering periods. Yet another source of trouble is that the times of opening and closing vary with the latitude in which the plants are growing, often also with the kind of weather prevailing at the time. There is, moreover, an unfortunate gap between noon and about 6 p.m. during which no plant normally opens or closes its flowers. These various difficulties and uncertainties have prevented floral clocks from being altogether successful, although it remains true that if the appropriate plants are at hand and one knows their behaviour in regard to opening and closing of flowers in the locality at the time of year that the observation is made, a fair idea of the time of day can be deduced by observing the behaviour of the flowers.[1]

Of more practical use is the information given by the so-called 'compass plants'. Of these, the two best known are the Wild Prickly Lettuce (*Lactuca Scariola*) of central Europe and the Rosin Weed (*Silphium laciniatum*) of North America, both belonging to the large and widely distributed family of Compositae. These plants carry their leaf blades in a vertical instead of a horizontal plane, in such a way that the leaf edge is presented to the noonday sun. From the plant's point of view, this arrangement may be regarded as advantageous in a dry sunny climate because a maximum leaf surface is exposed to illumination morning and evening when the intensity is low, whereas at midday when the illumination is greatest and might be damaging, the leaf presents its edge only. The result of this leaf arrangement is that the leafy shoots have a flattened appearance as though they had been put in a press and then planted with the plane of compression directed north and south (fig. 1). These flattened plants stand out conspicuously among the other components of the vegetation with radially disposed leaves, and serve to give a compass direction that might prove of use to anyone traversing a featureless prairie on a cloudy day when the sun provides no guidance.

[1] A floral clock constructed to indicate the month of the year, based on the fact that particular plants start flowering at a definite time of year, has been devised by Dr. J. R. Baker, and is described in *Jour. Roy. Hort. Soc.* 65, 306, 1940.

By way of contrast may be mentioned the unicellular green alga *Pleurococcus* which may serve as a plant guide under woodland conditions. *Pleurococcus* in damp temperate climates forms extensive colonies in the form of green films on tree trunks, fence posts, and similar objects. In north temperate latitudes, this develops mainly, if not entirely, on the north side where the trunks are never exposed to strong sunshine; by noticing which side is the greener and therefore towards the north, it is easy to steer a compass course.

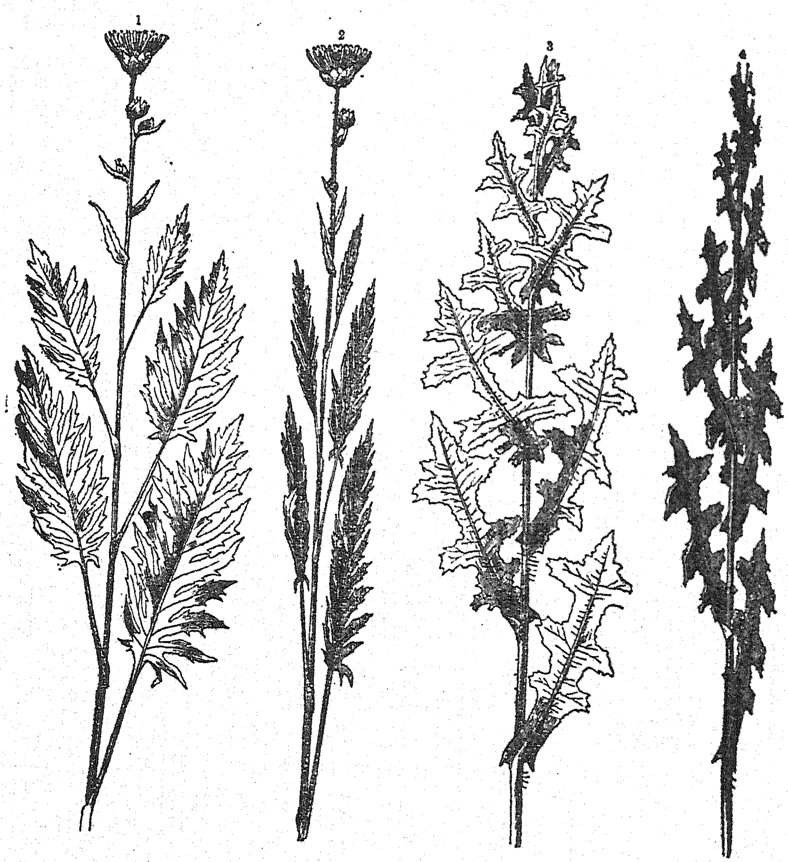


FIGURE I

Compass plants. From left to right: *Silphium laciniatum* seen from the east; the same plant seen from the south; *Lactuca Scariola* seen from the east; the same plant seen from the south.

Plants as historians

The information given by plants concerning the history of the site on which they are growing is often of special interest because they may be the main or even the only source from which such information can be obtained.

Every site, given time, acquires a typical grouping of plant species. Once established, it may be a long time before all traces of such vegetational associations disappear or can be removed so completely as to be undetected by a trained observer. This is partly because a species, once firmly in possession of a site, is difficult to dislodge so long as conditions do not become actively hostile; it has the advantages that go with possession, such as crowding out competing seedlings by rapid vegetative growth or swamping them by the abundance of its own progeny. Different types of plant associations may lead also in course of time to the production of particular types of soil, each with its own specialized population of animals and micro-organisms. Even if certain of the dominant plant species are removed, as when the trees in a woodland are felled, thus drastically altering the conditions of light, humidity, etc., to which the remaining plants are subjected, resistance to eviction is exhibited by many members of the established flora. When we find such typical members of a woodland ground flora as the Blue Bell (*Endymion non-scriptum*), Wood Spurge (*Euphorbia amygdaloides*), Wood Sanicle (*Sanicula Europaea*) and others growing on open ground, we can feel sure that, whatever may be the present condition of the site, at some time in the not far distant past it was occupied by trees.

The capacity of the soil to retain the effects of past treatment is all too evident to anyone who tries to lay down a lawn on a piece of land traversed by an old field path. Even if the ground is well cultivated before sowing with grass and a uniform sward apparently obtained, yet in times of drought the position of the old path will probably show clearly for many years as a strip of somewhat different colour. The character of the soil within the limits of a pathway becomes altered, primarily as the result

of consolidation which modifies the water-holding capacity of the soil; slight differences in this respect are not evident when there is an abundant supply of water everywhere, but only in times of drought when the water supply in the soil is reduced to a critical amount. The vegetation establishing itself on the path and elsewhere will tend in time to differ in relation to the critical demands for water of the plants composing it, and also with regard to the extent to which different plant species can withstand trampling. The persistent nature of such effects is often well shown in chalk down country where prehistoric trackways become clearly defined in early summer as white strips owing to the greater abundance of daisies.[1] At other seasons of the year the turf may appear uniformly green and only careful examination of the herbage will show that the proportion of some plant species, such as daisies, is higher in the trackways than elsewhere. Slight variations in tone, hardly perceptible nearby, may become readily distinguishable at a distance, so that these ancient trackways are often clearly visible from the air even at midday. (Aerial photographs to show earthworks and similar prehistoric features are usually taken with the sun near the horizon so as to emphasize differences in level by the shadows thrown; differences in tone are seasonal or depend on weather conditions.)

Turning to quite another kind of record from the past, study of the growth rings of trees may throw interesting light on the climatic conditions of earlier decades or centuries. In temperate or other climates with marked alternation of seasons, the kind of wood formed at the beginning of the growing season when growth is vigorous differs from that formed at the end of the season when growth has become sluggish. The juxtaposition of the two kinds of wood formed during successive seasons is evidenced in a cross section of the stem by the appearance of a ring, the distance between one ring and the next representing, as a rule, the amount of wood added to the girth of the stem during one growing season (Pl. 4; facing p. 28). Now the amount of new wood made by any tree varies from year to year, depending on

[1] Hubbard, A. J. and Hubbard, G. *Neolithic Dew-ponds and Cattle-ways.* Longmans, Green and Co. (Figs. XIX and XX.)

how favourable or otherwise the season was for growth. In good years much wood is formed and the annual rings laid down in the stem are wide; in bad years, on the other hand, the annual rings are narrow. Assuming that a single ring is formed in each growing season, it is possible by counting from the last-formed ring nearest the bark to compute the age of the tree from the total number of rings. It is not without interest that this possibility was first suggested by Leonardo da Vinci (*c.* 1505). Moreover, it is possible to determine the year during which any particular ring was formed and judge from its width whether this year provided good or bad conditions for tree growth in the district.[1]

As an example of the practical use of data of this kind may be cited the preliminary survey carried out by the Tennessee Valley Authority in the United States of America over the large area under their control. Examination of the annual rings in a large number of trees in different parts of the area provided data as to the variations in the amount of rainfall in successive past years. The information so acquired provided a basis for estimating the amount of rainfall to be expected in the future, in particular, *the maximum number of wet seasons likely to occur in succession*; upon these estimates were based the engineering works for water control.[2]

How far into the past these seasonal records of annual rings can be followed depends upon the age of the tree; this may extend to hundreds of years, although the reputed age of 4,000 years of some of the Big Trees (*Sequoia gigantea*) of California is probably an over-estimate.

An obvious pitfall in drawing deductions of this kind is that the annual rings in the wood of a tree reflect not only seasonal variations but other changes in the environment, as well as the vicissitudes suffered by the individual. Should a tree lose its foliage in early summer by some accident, such as a forest fire or an attack by caterpillars, this event will be recorded in the wood by the formation of only a narrow ring, however favourable for growth may be the season; should the mishap occur early

[1] Glock, W. S. 'Growth rings and climate.' *Bot. Rev.*, 7, 649, 1941.
[2] Lilienthal, D. E. '*T.V.A.—Tennessee Valley Authority.*' Penguin Special S.151, 1944.

enough for the tree to form a new crop of leaves, two narrow rings may be formed that year. To avoid being misled by such individual memoranda, any general deductions from the character of annual rings must be based on critical examination and comparison of the rings in the wood of a number of trees growing in the same locality.

A convenient way of recording the annual amount of wood formed by a tree in successive years is to draw a number of equidistant vertical lines on a horizontal base, the length of each line representing the width of an annual ring in a particular year. The variation in the lengths of these vertical lines (and so in the widths of the annual rings) from year to year over any period of time will be more obvious if lines are drawn connecting their upper ends, the whole forming a 'graph' (fig. 2A). If one tree grows faster than another, i.e. forms secondary wood at a greater rate, the average length of the vertical lines will be greater in the former case and the graph will be farther from the horizontal datum line; but there will be corresponding variations in the lengths of the lines from season to season in each. In other words, the graph may be near or far from the zero datum line, depending on whether growth is slow or rapid, but its *form* will be essentially similar for all trees growing in the same district as far back as the age of any tree allows it to be followed.

Graphs of this kind, showing the comparative widths of annual

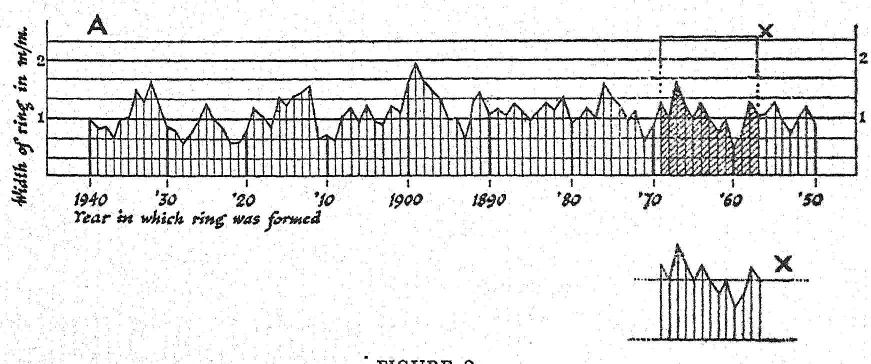


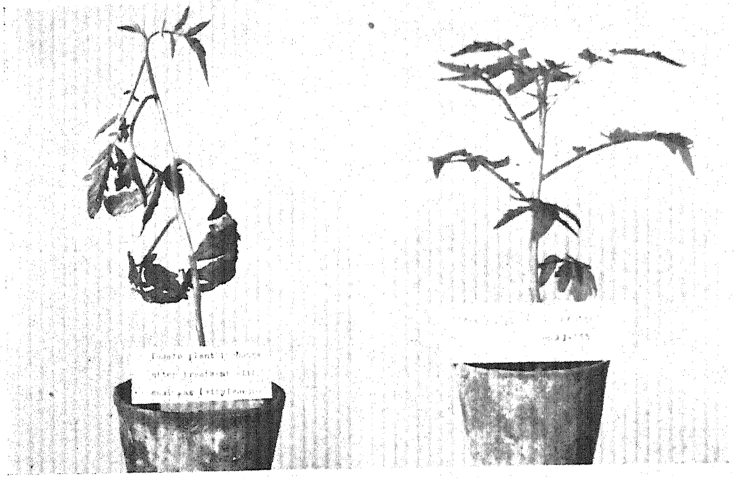
FIGURE 2

Diagram showing yearly increments to width of wood in a tree from 1850 to 1940. Explanation in text.

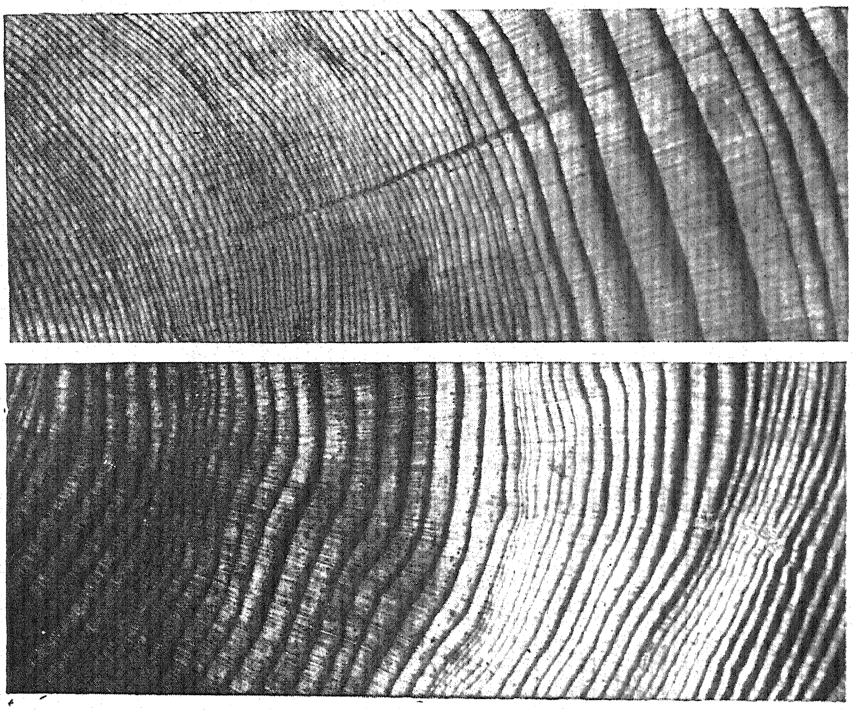
rings formed in successive years by trees growing in a district have been used to check dates ascribed on other grounds to archaeological remains. Thus, if a piece of timber forming part of a building or of some utensil is available, a cross section of the wood is made, the widths of the annual rings measured and recorded in the form of a graph (fig. 2, X). This is then compared with the complete 'standard' graph of living trees in the locality. It may be found that the former matches in shape some part of the latter. Should this be the case, it at once becomes possible to say in what years the annual rings in the piece of wood forming the specimen were laid down and so put a limit to the age of the building or utensil of which the wood formed a part, for this clearly cannot antidate the time at which the wood was formed.

Plants may provide a vast amount of information about their own family past. Under favourable geological conditions the hard or skeletal parts may be preserved as fossils and retain their original structure in considerable detail. Examination of such fossil remains provides data from which the structure and habits of plants of past ages can be reconstructed, and the evolutionary tendencies in different groups worked out; they may also throw light on the nature of the climate at the time the plants were growing. Such fossil records are of necessity very incomplete because it is only under favourable and rather exceptional conditions that dead plants survive decay and mechanical disintegration, and retain their tissues in recognizable form. Obviously it will be the woody and other skeletal tissues that tend to be thus preserved, the softer and more delicate parts being lost.

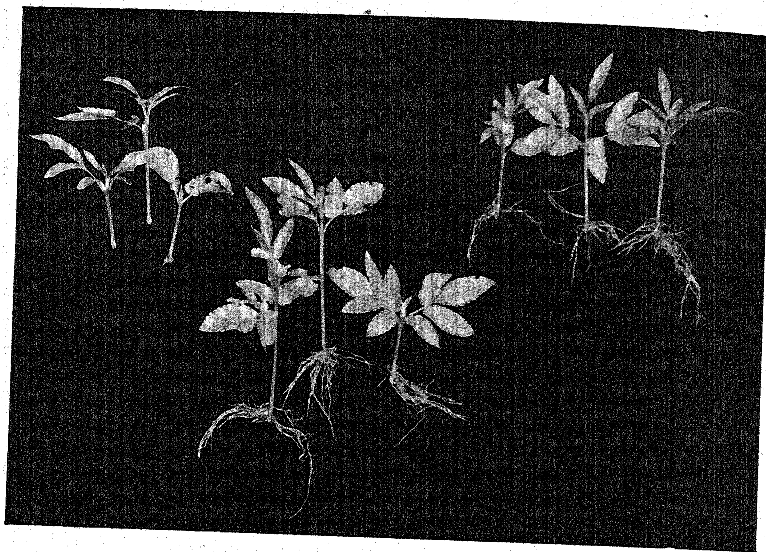
Owing to their resistant—cutinized—outer coat, pollen grains are among those parts not infrequently found in recognizable condition long after the death of the plants that produced them. Moreover, the pollen grains of different kinds of plants are very distinctive in appearance, showing a great diversity in size, shape and superficial patterning, so that it is often possible to deduce from a single pollen grain the presence, if not of the species, at least of the genus to which the plant producing it belonged (fig. 3). Deductions of this kind have been particularly successful in the case of fairly recent geological deposits such as



3. Reaction of tomato plant to traces of coal gas (ethylene). The plant on the left shows the positions assumed by the leaves twelve hours after exposure to traces of coal gas containing ethylene; that on the right the position in which the leaves are held normally.



4. Cross sections of wood of coniferous trees showing 'annual rings'. The wood formed each spring is softer and lighter in colour than that formed later in summer. That below is from a tree growing under natural conditions, the variations in width of the rings reflecting the extent to which successive growing seasons were favourable or the reverse. That above is from a tree growing in a wood in which thinning operations were carried out. The abrupt change from narrow to wide rings indicates the greater vigour of growth induced by the more favourable con-



(i) (ii) (iii)

5A. Growth substances and the rooting of cuttings. Cuttings of *Eucryphia glutinosa* treated in July: (i) controls; (ii) naphthaline-acetic acid one thirty-thousandth for twenty-four hours; (iii) indole-butyric acid one sixty-thousandth for twenty-four hours. Photographed eight weeks later.

(i) (ii) (iii)

5B. Cuttings of tree ivies treated in January: (i) controls; (ii) indole-acetic acid one ten-thousandth for twenty-four hours; (iii) naphthaline-acetic acid one ten-thousandth for twenty-four hours. Photographed three weeks later.

peat bogs. Samples of the peat are suitably prepared and examined with the aid of a microscope; from these observations records are compiled indicating the kinds of pollen grains present and their relative abundance. From such records it is

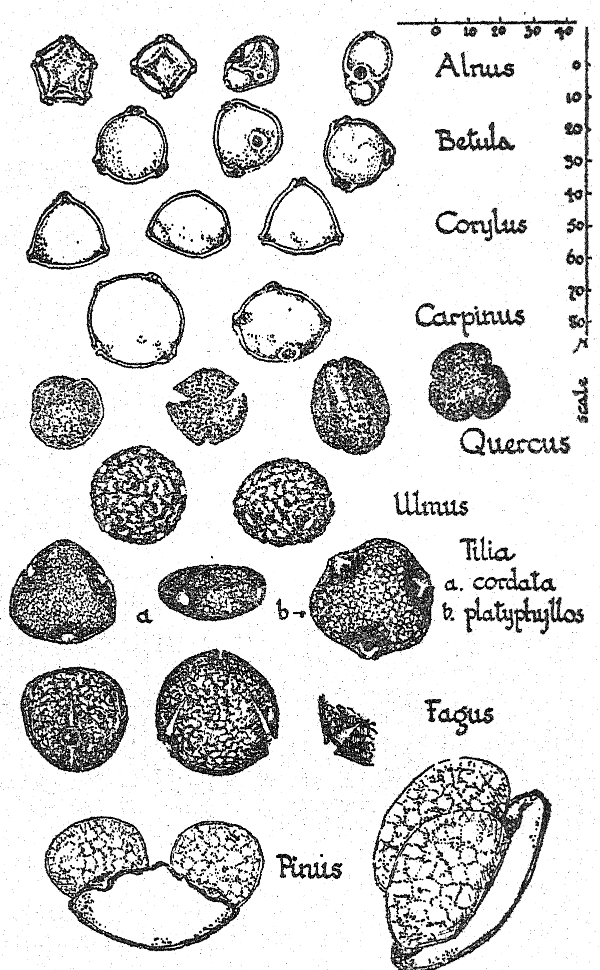


FIGURE 3

Diagram to show the salient characteristics of the pollen of the chief genera of trees represented in British post-glacial deposits. The grains are shown as they appear in the subfossil state; they are all drawn to the same scale, and views from different angles are presented so as to give an idea of the solid shape of each grain.

possible to estimate the relative proportions in which certain species of plants were present at the time the peat was laid down, and to compare this with the relative abundance of the same species at the present time. Since newly formed peat is deposited at the surface, by carrying out similar observations on selected samples taken from different depths below the surface, it may be possible to follow the vegetational changes that have occurred during the period when the peat was accumulating, and to deduce probable changes in climate during this period. This special kind of investigation is referred to as 'pollen analysis'.[1,2]

Much special knowledge and experience is required in order to interpret such records correctly; it cannot be assumed, for instance, because one kind of pollen is more abundant than another in a peat sample under examination that the species of plant producing this pollen was also more abundant than other species, because an abundance of pollen may mean only that this particular species was more prolific in pollen production than its neighbours. When suitable allowances have been made, however, the technique of pollen analysis has proved reliable and has been very fruitful in throwing light on changes in the vegetation that have come about in the geologically recent past. The limits of application of the method are definitely circumscribed; it can give information only about pollen grains identified as similar to those of known species, and in practice is limited to plants that broadcast relatively enormous quantities of pollen and depend on wind currents for its distribution—the so-called wind-pollinated or anemophilous plants—to which category belong a large proportion of our native forest trees.

For example, you can decide whether Birch or Alder are now more or less abundant in a district than when either of them first appeared in the locality; it is useless expecting to learn much about the distribution of Cherry, Buttercups or other species with insect-pollinated flowers by such methods. The accompanying diagrams illustrate how the results of pollen analysis are recorded and how they may indicate the rise and fall in fre-

[1] Godwin, H. 'Pollen analysis.' *New Phyt.*, *33*, 278, 325, 1934.
[2] Godwin, H. 'Studies of the post-glacial history of British vegetation.' *Phil. Trans. Roy. Soc.*, *230*-B, 239, 1940.

quency of different species in a particular area during the period of time taken for the peat to accumulate (figs. 4 and 5). Similar records obtained from peat deposits elsewhere provide the materials for the compilation of a map showing the distribution of certain species in the country as a whole at different periods in the past, making it possible also to determine when a species

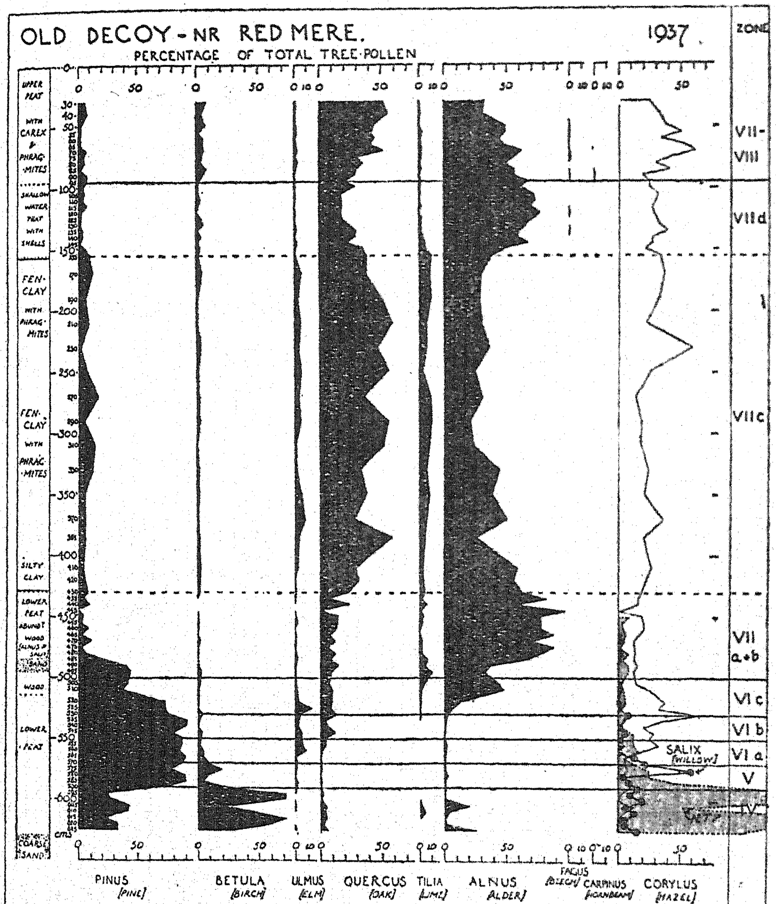


FIGURE 4

Pollen diagram for Old Decoy in the natural channel of the river Little Ouse, near the landward termination of the fen clay. The curve marked N.T.P. shows the ratio of non-tree pollen to tree pollen below 450 cm.

first reached the area studied, and where it first gained a foothold.

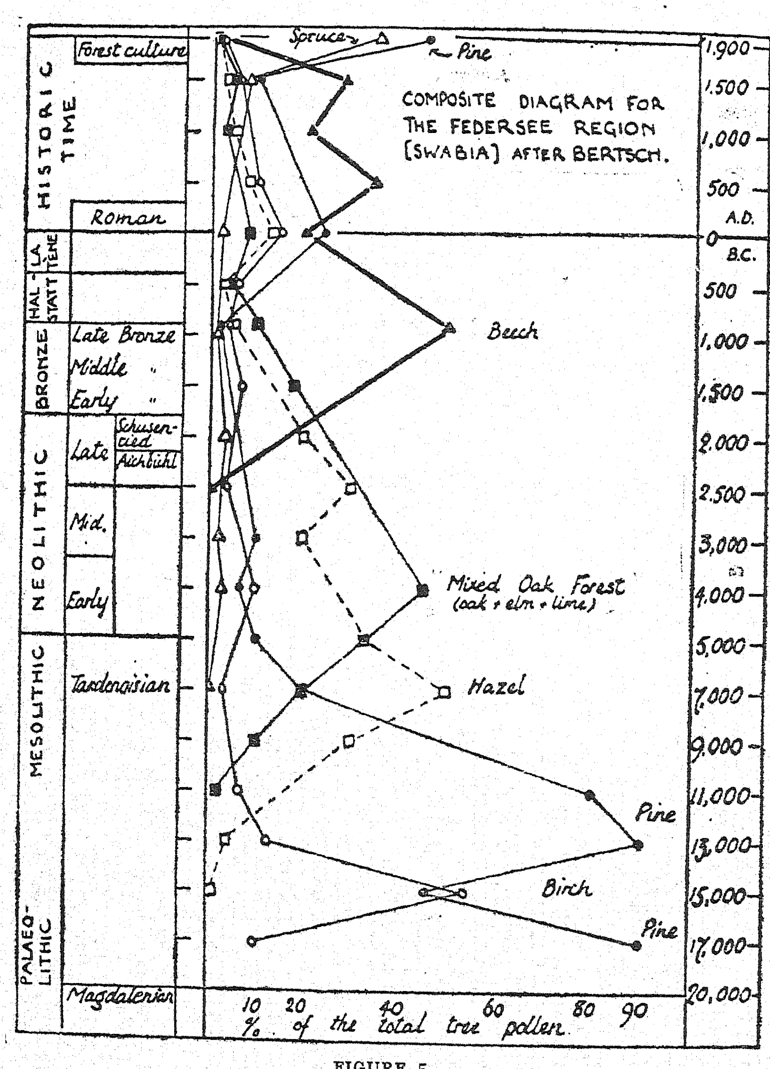


FIGURE 5

Composite pollen diagram for the deposits of the Federsee region of Swabia, south Germany. It is based on analysis of a large number of vertical series of peat samples, and is very closely correlated with the very abundant horizons of human occupation which occur stratified in the lake deposits. After Bertsch, reproduced by permission from Steers, *Scolt Head Island.*

The facts to which attention has been drawn in this chapter serve to remind us that in spite of the slowness with which, as compared with animals, plants react to changes in their environment they nevertheless exhibit a high degree of sensitiveness and discrimination if given time to register their responses.

It is inevitable that we should look out upon the world with a greater or less degree of egocentric vision. We instinctively assume that our fellow men and the various animals we see moving about are actuated by motives similar to our own: in doing so we frequently misunderstand our own kind and almost always humanize animal behaviour to a quite unwarrantable extent. The rest of our surroundings we are apt to regard as the general furnishings of the world, a sort of stage setting in which we and the animals play their part—rocks and rivers, mountains, trees and other plants making up the 'set'. It is hoped that the survey given in the foregoing pages may have persuaded the reader that plants, like ourselves, react as living organisms to their environment although in very different manner, indicating by their reactions 'awareness' of their surroundings and ability to exercise some power of choice. Not only do the structural features and manner of growth of living plants record their individual experiences, but the same is true of their predecessors when preserved as fossils, so providing the materials from which can be surmised the conditions under which these plants were living in the distant past. Comparisons between living and fossil forms can be used, moreover, to assist in determining the evolutionary history of the groups to which they belong, and so help to establish affinities between members of the present-day flora.

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Chapter 2

COMPOSITE PLANTS—CHIMAERAS

Development in plants and animals

Except in the simplest forms and the earlier stages of development of those more highly organized, there is a fundamental difference in the manner of growth of plants and animals: the adult stage, a growth phase so definite and final in the case of most animals, has no real counterpart in plants. It is true that in both, life begins as a single cell, the fertilized egg-cell, and that in both plants and animals early development up to a juvenile stage is the result of generalized cell divisions; but from this point onwards there is divergence in behaviour. In the animal, growth of the same kind continues until there results an adult individual of fixed and definite size, after which further growth activities are limited almost exclusively to the carrying out of repairs.[1]

[1] Admittedly, some animals, such as fishes, may continue to increase slowly in size after reaching maturity, but even so any such growth remains generalized. That fish have not a fixed adult size is no doubt connected with the fact that they are water-borne and thus relieved from the necessity of supporting the weight of their body against the pull of gravity. In a land animal, any considerable increase in size above the normal would call for modification of the structural form appropriate to a particular size. For example, if the linear dimensions of an animal are doubled whilst retaining the same relative proportions, the weight will be increased eight times (2^3), since this is directly related to volume, but the strength of the supporting skeleton only four times (2^2), since this depends on the area of the cross section of the bones. Thus, the larger the animal the more massive must be the supporting limbs, a relationship illustrated by the columnar legs of the elephant and the slender legs of the deer.

In the plant, on the other hand, after an embryonic stage, and in general very early in development, growth becomes restricted to definite regions. In stems and roots, for example, the production of new cells contributing to growth in length is strictly confined to the tips of these organs, to the so-called 'growing points' or 'apical meristems': growth in thickness may occur later in many plants as a result of awakened activity of cells in other, more deeply seated, positions. These regions of growth, or 'meristems', may remain active indefinitely, additional ones repeatedly arising for the organization of lateral branches, lateral roots and other new structures. There is, thus, no fixed and definite standard size to which all members of a single plant species conform—each individual continues to grow and increase in size until mechanical or physiological factors put an end to further increase. A palm tree, for example does not attain a standard size when mature and then cease to grow as is the case with a blackbird or rabbit; the stem continues to elongate until retarded by the difficulties of transporting water to leaves at ever-increasing distance from the soil, or until the lengthened stem results in the tree being blown down in a gale, or some other accidental cause brings growth to an end. In fact, instead of growth in size slowing down to a minimum or ceasing altogether on reaching the adult stage as in animals, the tendency in plants is rather for the rate of increase to accelerate with increasing age since the latter is accompanied by the appearance of additional growing regions. This tendency is checked eventually, not by an inherent loss of capacity for the production of new tissues on the part of the growing regions, but by the development of factors adverse to growth resulting from increased size. Among such factors are the difficulties of transporting water and nutrients over ever-longer distances, the decreased supplies of oxygen reaching living tissues that lie farther beneath the surface, and the inadequacy of the mechanical structures in the shoot to support the growing bulk of the plant.

As a consequence of this fundamental difference in the manner of growth, an adult animal consists of tissues that, with the exception of those forming part of the reproductive system, are

all fully mature, whereas an adult plant, in addition to these, possesses throughout its life juvenile tissues resulting from the persistent activity of the cells in its growing regions.

Ageing

As a further consequence, entirely different concepts are involved when considering 'ageing' in animals and plants; often indeed the same concepts cannot be employed when comparing two kinds of plants.

The adult tissues of the animal body gradually 'age', that is, become less efficient in their functioning with long-continued activity. This is partly because the chemical conversions upon which vital activity depends may result in time in an accumulation of by-products sufficient to impede essential chemical reactions. Finally, one or more of the tissue-systems reaches a stage of ill-functioning so advanced that co-ordination of the life processes as a whole is thrown out of gear and the organism dies of 'old age'. In a perennial plant, the earlier formed tissues undergo a similiar process of ageing, ending ultimately in death, but this does not necessarily result in death of the individual because later-formed, more juvenile tissues continue to function in full activity. In some cases the older dead tissues may quickly rot away, in others they may be resistant to decay and accumulate in course of time to constitute the main bulk of the plant.

The underground horizontally growing stem of a perennial grass will serve as an example of the first case. Here the growing region at the tip is continually forming new young tissues to take the place of the older part of the stem as it ages, dies and eventually decays. Although individual cells have a limited life-span, the stem as a whole has an unlimited capacity for growth and, as a result of branching, tends to occupy an ever-increasing area.

By way of contrast, in trees the old dead tissues do not for the most part usually decay readily but persist as a result of impregnation with preservative substances produced by the tree itself. Thus, in an old tree, the centre of the trunk is usually dead, forming

the so-called 'heart-wood'; the living part of the wood comprises only a narrow outer sheath which continues to function indefinitely. Although cells on the inner side of the sheath are continually dying and thus adding to the volume of dead heart-wood, fresh contributions of young cells are constantly added to the outer side of the sheath from the growing region or 'cambium'. Theoretically, therefore, a perennial plant has an indefinite span of life, provided that continued increase in size does not seriously impair its ability to obtain nutrients, and that the individual escapes death by accident or disease.

In nature, this unlimited capacity of Flowering Plants to continue active growth finds expression in various forms of vegetative propagation as in the production of bulbils, offsets, tubers and so on; in horticulture, these methods of multiplication are supplemented by such artificial devices as gardeners use in grafting, budding, and the taking of cuttings and layers. Many plants have been propagated in this way for a long period of time.

It has been held that plants propagated solely by such vegetative means sooner or later degenerate, and that periodic reproduction by seed is required for rejuvenation. While there is no doubt that varieties of potato, raspberry and many other plant species do degenerate when propagated only by vegetative means, such cases are now interpreted as due to an accumulation of 'virus diseases' in the tissues, the rejuvenation that occurs in seed production being accounted for by the fact that such virus diseases are rarely transmitted through seeds.[1] The correctness of this interpretation may be illustrated by the following facts. A crop such as potato if originally free from virus becomes infected so rapidly when grown in most districts in England that the bulk of the tubers carry some form of virus disease by the end of the first growing season. Such tubers, if used for producing next season's crop, give rise to diseased plants with a much reduced yield of tubers. Again, so serious and widespread has attack by virus diseases become in raspberry that wild raspberry is dying out in many districts

[1] The nature of virus diseases is explained on p. 60.

where previously common. In order to obtain healthy raspberry plants for the garden, plants are now raised from seed; the usual method of propagation by young shoots or 'canes' has been to a great extent abandoned in large-scale cultivation since it is difficult to find mature plants free from infection. In these examples, the 'degeneration' that occurs after a short period of vegetative growth is undoubtedly to be ascribed to the rapid spread of virus infection from plant to plant rather than to any failure in vigour of the growing region as a result of continued vegetative activity. They are no doubt extreme cases, but similar causes may underlie the 'degeneration' observed in other plant species less highly susceptible to virus diseases.

In general, it may be concluded that there is no good evidence that physiological ageing occurs in perennial plants, or that there is necessity for rejuvenation through seed production except as a means of freeing a plant from contamination by virus diseases. Individual tissues age and die, but a perennial plant—indefinitely and with undiminished vigour—continues to produce new juvenile tissues to take their place.

The foregoing remarks apply to perennial Flowering Plants as a whole, a majority of them producing seeds repeatedly without any evidence of injury to the individuals concerned. Some Flowering Plants, however, die as soon as they have become fully mature and produced one crop of seeds. In annuals, seed production followed by death occurs normally at the end of the first growing season; in biennials, at the end of the second growing season; in a few perennials, such as the Century Plant (*Agave* spp.) seed production and death may be postponed for twenty or more years. Species that behave in this way are referred to as *monocarpic* because they produce but one seed-crop; whether annual, biennial or perennial, the individual plant always dies after seed production.

Two theoretical explanations have been offered to account for death after a single flowering and production of seed: one, that starvation follows the rapid utilization of food reserves during formation of the seeds, the other, that during the process of seed formation poisonous substances are produced. Neither

explanation can claim to be supported by satisfactory evidence; decision as to which, if either, is correct must await the results of further research.

It may be noted that some perennial plants of this kind, before they have reached the flowering stage, produce vegetative offshoots. Thus although the main part of the plant may die after flowering, these offshoots persist, so that through them the 'individual' escapes death. It has been found also that by suitable control of cultural conditions the production of flowers may be accelerated or prevented: annuals may have their life-span lengthened indefinitely, biennials may be converted into annuals or perennials, and the usual duration of life of perennials may be extended or curtailed (pp. 104 seq.).

The capacity for vegetative reproduction possessed by perennial plants calls for a far wider conception of what constitutes an individual than that found adequate when considering the higher animals. For example, rhizome of Iris in its forward growth may fork; the branched rhizome is still to be regarded as the plant individual. Later, the older part of the rhizome may die and decay, so isolating the two branches from one another. Are these two branches to be looked upon as two 'individuals' or as parts of one 'individual' that have become separated as a result of the manner of growth natural to such rhizomes? To avoid ambiguity, separate plants that have originated from a common source by vegetative propagation are described botanically as belonging to the same *clone*; since they are, in fact, the separate and dispersed parts of a single individual they will all possess identical hereditary traits (apart from the occurrence of vegetative mutations), and these common traits may differ from those of members of other clones, just as one person differs from another. For example, all the plants resulting from cuttings taken from a single plant belong to the same clone.

This dispersed individuality is not found in the higher animals because these lack the capacity for vegetative reproduction, which occurs only among certain more lowly animal groups.

It may be said that, in effect, a capacity for vegetative repro-

duction confers potential immortality on those organisms possessing it.

The growing apex

Returning to consideration of the manner in which growth occurs in the Flowering Plants, it is evident that the whole mechanism responsible for elongation of stem and root is centred on the growing regions at the tips of these organs; throughout life, so long as conditions remain favourable, the cells constituting these growing tips continue to divide and form new tissues which, in course of time, become incorporated into the adult structure of the plant. Since the growth of plants so largely depends on the activity of these apical growing regions, it is but natural that considerable study should have been devoted to interpreting their structure and behaviour.

The stem apex of a Flowering Plant has the form of a blunt cone, consisting, as microscopic examination shows, of a mass of small cells all alike and in process of division. Of the new cells so formed, those towards the apex continue to divide actively, whilst most of those more distant from the apex gradually lose the capacity for division, become altered in various ways and form finally the mature tissues of the young stem. At certain points along the sides of the stem apex, however, small groups of cells retain their power of active division and constitute new centres of growth that become responsible for the production of outgrowths such as leaves and lateral branches (fig. 6).

In Dicotyledons and Conifers, some of the more centrally placed cells of the growing apex also retain their capacity for cell division, constituting the 'cambium' of the mature stem; the increase in diameter of the stem at a later stage of growth referred to as 'secondary thickening' originates from the renewed activity in division of these deep-seated cambial cells in which activity neighbouring cells between the bundles cooperate.

According to modern views, the cone-shaped tip of the vegetative stem behaves as though it were built up of a series of sheaths or skins, each one cell-layer thick, overlaying a central

core. The central core and the successive outer sheaths form an organic whole, each maintaining its own individuality during growth and each responsible for the production of some particular region of the mature shoot system. The number of such layers recognizable at the growing apex varies with the kind of plant; two are usually clearly defined, sometimes there is a third or fourth, less readily distinguishable, before the central core is reached (fig. 6).

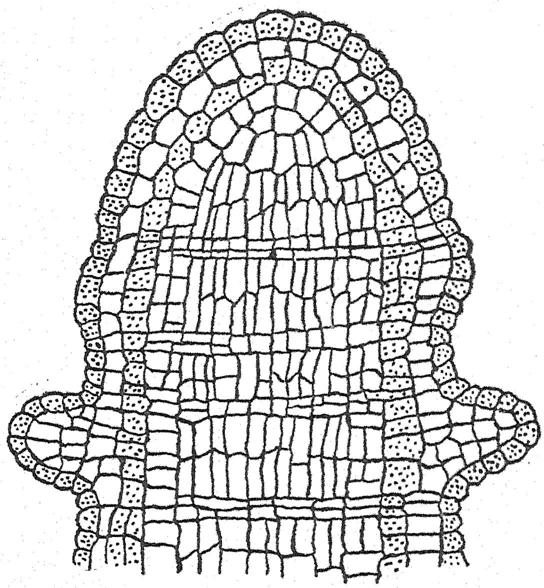


FIGURE 6

Growing apex of the shoot of *Hippuris vulgaris*, a British water plant. The first and third layers of dividing cells at the tip and the tissues to which these respectively give rise have been stippled to distinguish them from the rest of the tip and its products. It will be noted that the outermost layer of dividing cells gives rise to a single layer—the epidermis—covering the mature shoot, and that the second layer of dividing cells forms a subepidermal layer one cell thick except in regions of leaf formation where localized activity of division occurs. The bulk of the leaf tissues are thus derived from the second layer of the stem tip; the same is true for the lateral buds arising subsequently in the leaf axils.

The regions of the mature plant body derived from each of the zones also vary with the kind of plant. In the majority of

Flowering Plants the outermost layer of the growing tip is responsible for forming an external 'skin' one cell thick, the epidermis, and makes no contribution to tissues within it. The second layer of the growing point usually gives rise to a tissue consisting of a single layer of cells immediately beneath the epidermis. Typically, therefore, the first and second layers of the growing apex give rise to the two outermost cell layers of the young stem, the central region or core being responsible for all the other mature tissues in the stem.

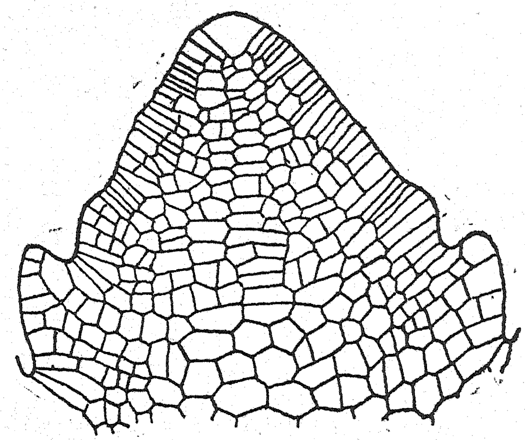


FIGURE 7

Diagrammatic drawing of the stem apex of Horsetail (*Equisetum* sp.). Note the single dividing apical cell from which all the mature tissues are derived.

The edge of the leaf and certain other parts of the plant have a rather different derivation from that described for the stem. Towards the edge of the leaf those cells derived from the second skin of the growing point divide in all directions to form a tissue several cells in thickness. The nearer to the leaf margin, the more marked is this behaviour; in fact, for a distance from the margin varying with the kind of plant, the whole of the leaf tissues, apart from the epidermal covering, may be derived entirely from the second layer of the growing apex. The typical way in which the successive layers of dividing cells at the stem apex contribute to the different regions of mature stem and leaf is indicated in the diagrams on p. 46 (fig 9).

In plants ranked below the Conifers and their allies, the growing points have a much simpler structure, all new tissues being traceable to the activities of a single dividing cell (fig. 7).

Plant chimaeras

These rather complicated anatomical facts are necessary for a proper understanding of the nature of certain remarkable plants of composite origin.

As might be expected, the tracing backwards of tissues in any part of a mature plant to their origin at the growing tip involves laborious microscopic investigation. The same information may often be obtained with less labour and greater certainty if the plant is known to have a special kind of composite structure.

One kind of composite plant is familiar to everyone in the form of garden varieties of fruit trees and roses grafted on different stocks. Another less familiar kind is that in which the growing apex itself is of composite structure, one or more of the various skins or the core differing from one another in respect to the plant species or varieties from which they are derived. Plants possessing composite growing points of this kind are included under the general name of *plant chimaeras*.

For example, cases are known in which the nuclei of the cells that constitute the second 'skin' are larger than those of the cells in other parts of the growing point. Any tissues of the mature plant derived from this second layer can be at once recognized microscopically by the presence of larger nuclei, and the contributions thus made to the mature tissues by the second layer easily determined (fig. 8). In general, if any layer of the growing apex possesses nuclei distinctive in character, the contributions of this layer to the total growth can be readily traced.[1]

None of the many and various combinations that have been observed illustrate the characteristics of plant chimaeras more simply and obviously than those in which the growing apex is

[1] Satina, S., Blakeslee, A. F. and Avery, A. G. 'Demonstration of the three germ layers in the shoot apex of *Datura* by means of induced polyploidy in periclinal chimaeras.' *Amer. Jour. Bot.*, 27, 895, 1940.

made up of two components, one of which has the capacity of producing chlorophyll and thus becoming green at maturity, and the other has not. Let us first consider chimaeras of this kind: as objects for study they have the advantages that the products from the two components of the growing tip are either green or colourless and therefore readily distinguishable, that they are commonly met with in gardens and that they can be usually recognized at a glance since, as will be explained, they often possess variegated foliage.

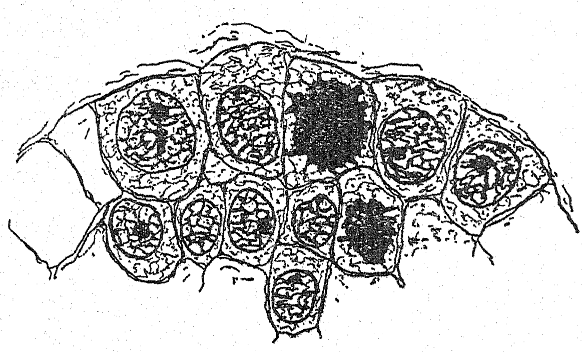


FIGURE 8
Part of the growing apex of a chimaera composed of *Solanum lycopersicum* (Tomato) except for the outermost layer derived from another species, *Solanum memphiticum*. The Tomato possesses nuclei with 24 short chromosomes, the other species has nuclei with 48 long chromosomes. In the resting stage the nuclei of the former are obviously smaller than those of the latter, so that it is possible to recognise any cell in the mature tissues derived from the outer layer by noting the larger size of its nucleus. Two of the nuclei are shown in a state of division.

The cells of flowering plants contain small granules or specialized fragments of living material known as *plastids*. These are of several kinds, only those known as *chloroplasts* being able to develop the green pigment chlorophyll under appropriate conditions. The green parts of plants owe their greenness to the presence in their cells of large numbers of this special kind of plastid; the non-green parts of a variegated leaf lack chloroplasts although other kinds of plastids may be present; the latter may be responsible for colourless areas if they contain no pigments or for yellow areas if they contain such yellow pigments

as carotin to which the yellow colour of many flowers and of the roots of carrots is due.

A stem tip of which the central core possesses plastids capable of becoming green and of which the two outer layers lack plastids of this kind gives rise to a mature stem in which the central tissues are green but the two outer layers are colourless. The general effect is that of a green stem, the two colourless layers on the outside allowing the green colour within to show. This condition holds over the greater part of the plant. Towards the margin of the leaf, however, the tissues contributed by the second layer of the growing tip become increasingly important (p. 42), until at a distance from the margin varying with the kind of plant, the whole of the leaf tissue apart from the epidermis is derived from this source. Since neither of the two outer layers of the growing point possess the kind of plastid that can form chlorophyll, the margin of the leaf derived from them will be colourless. The type of variegated plant so frequently met with in gardens having green leaves with a white margin originates in this way owing to possession of stem tips of which the two outer cell layers lack chloroplasts; it is a special kind of plant chimaera in which the two outer layers and the core of the growing apex differ constitutionally in this respect (fig. 9: E to H).

The converse kind of variegation pattern—stems and leaves almost white except for a dark green margin to the latter—is rather less common but not infrequently met with. It is derived from a growing apex having the converse arrangement to that described above; namely, a core with plastids unable to develop chlorophyll surrounded by a two-layered skin of which the second layer at least (from which the bulk of the leaf margin is derived) contains chloroplasts (fig. 9: A to D).

It will be noted that in this common type of variegated plant it is the nature of the *second* cell layer of the stem growing apex that determines whether the border of the leaf is green or white; the outermost layer forming the epidermis is of little importance. This is because, in most flowering plants, apart from certain specialized cells, the conditions in the epidermal cells are unfavourable to the development of chlorophyll—or favour its

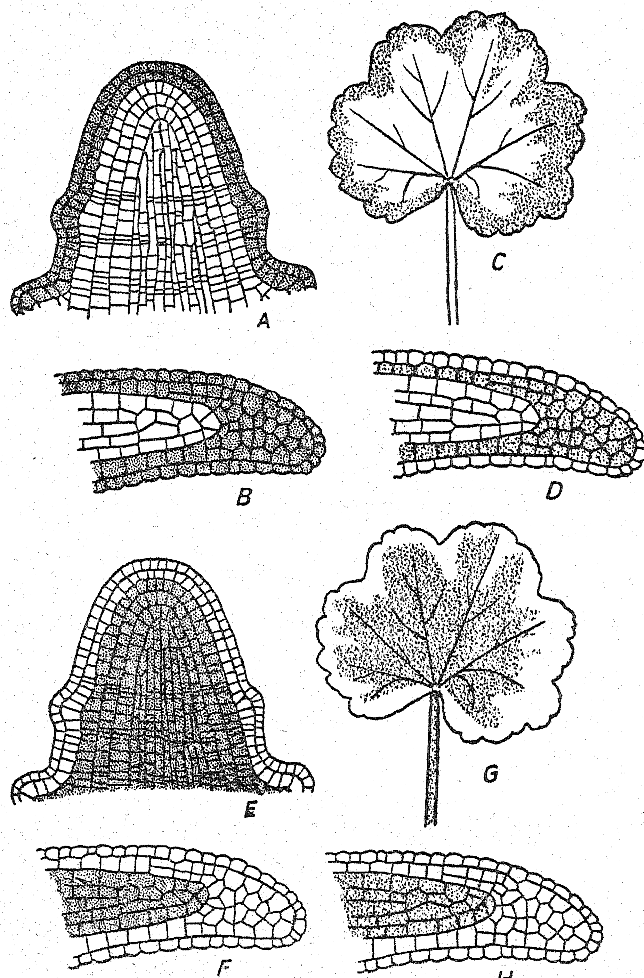


FIGURE 9

A—D, two-layered (dichlamydius) green-over-white chimaera. A, section of shoot apex showing two layers of cells with plastids capable of becoming green covering a core the products of whose cell divisions lack the capacity to form chlorophyll and are therefore colourless. B, transverse section of a leaf margin showing that the first and second layers of the apex organize the whole of this part of the leaf while forming only two layers over the centre part of the leaf. C, the superficial appearance of this leaf, a green margin to an otherwise white leaf. D, transverse section of margin of mature leaf; the epidermis remains colourless in spite of containing chloroplasts, conditions in the epidermal cells being unfavourable to the development of chlorophyll. The stippling in A and B indicates the location of chloroplasts, that in C and D the regions that actually develop chlorophyll.

E—H, the converse dichlamydius white-over-green chimaera.

destruction. As a consequence, whatever kinds of plastids it may contain, the epidermis is a non-green cell layer; any green colour the leaf may exhibit is derived from the tissues within.

These plants with variegated leaves which are structurally white-over-green or green-over-white chimaeras show certain peculiarities with respect to reproduction.

Stem 'cuttings' and grafts retain the characters of the plants from which they are derived, just as do the lateral branches of the parent plant; these are the usual means by which chimaeras are propagated. New stem structures produced by the parent stem or by a cutting or scion made from it are formed by the enlargement of a superficial bulge on the stem affecting the outer few layers of tissue only, in which the arrangement of the skins and core is usually maintained as in the original stem.

On the other hand, lateral roots are formed by the activity of deeply seated cells derived from the 'core' tissues; these organize the growing apex of a lateral root which then forces its way out through the more superficial tissues of the parent root or stem. Being derived entirely from the core region, these roots, if used for propagation by means of 'root cuttings', as can be done in some plants, give rise to individuals consisting only of core tissue, all trace of the chimaeral structure being lost (fig. 10). Thus a root cutting of a variegated chimaeral plant having a white margin to the leaf gives a uniformly green individual, while one from a plant with a colourless stem and green leaf margin yields a plant that is uniformly colourless. In the latter case the plant survives only so long as its reserves of food last, since in the absence of chlorophyll it is unable to manufacture fresh supplies.

A number of other cases are known in which plants derived from root cuttings differ from the 'parent' or from plants obtained from stem cuttings. If, for example, the horticultural variety of *Bouvardia* known as 'Bridesmaid' bearing pink flowers is propagated by root cuttings, in most cases the resulting plants bear dark red flowers resembling the variety 'Hogarth'. The explanation of such behaviour is that most of the strains of 'Bridesmaid' in cultivation are chimaeras, the outer skin consisting of a variety that develops a pink colour in the epidermis

of the flower petals, the core being made up of tissue belonging to 'Hogarth'. The root cutting originates entirely from core tissue and consequently bears the dark red flowers characteristic of the variety 'Hogarth'.

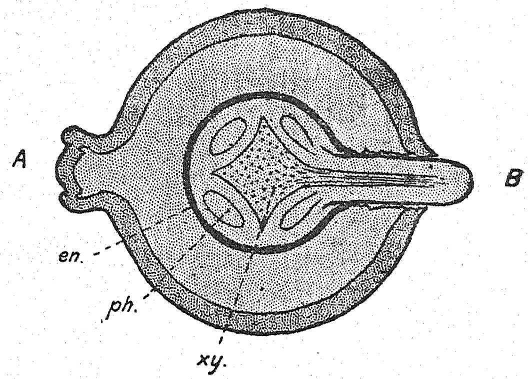


FIGURE 10

Transverse section through the main root of a chimaera having two layers of 'green' tissue overlying a core of colourless tissue. A, adventitious shoot bud—periclinal structure retained. B, lateral root—consists of core tissue only; used for propagation will yield plants that are entirely colourless.
en, endodermis; ph, phloem; xy, xylem.

As a result of extensive experiments in propagating various horticultural varieties of different species by root cuttings it has been found that quite a number of those normally propagated by stem cuttings have a chimaeral structure. Such constitution is maintained so long as stem cuttings are used as a means of increasing stock and may remain unsuspected until the different nature of the core is revealed in the process of obtaining root cuttings. In addition to varieties of *Bouvardia, Pelargonium* and *Nicotiana,* several commonly cultivated varieties of potato such as 'Golden Wonder' and 'Field Marshal' have been found to be chimaeras.

Seedlings from these variegated plants are usually, like root cuttings, uniform in colour. But whereas, for example, plants having white margins to the leaves give uniformly *green* root-cuttings, they bear seeds that grow into uniformly *white* seedlings; and vice versa. Thus the character of the seedlings follows

that of the leaf margin of the plant from which the seed is derived and is opposite in kind from that obtained in propagation by root-cuttings. Moreover, not only do seedlings show no trace of variegation, but it is immaterial whether the pollen is derived from a flower on a green, white or variegated branch; the kind of seedling obtained depends solely on the character of the seed parent. These results are explained by the fact that the sex cells in flowering plants produced in the ovules and anthers are derived almost without exception from the *second* layer of the growing point, and this, as we have learned, is also the layer that determines the character of the leaf margin. The purely maternal inheritance in this case is explained by the fact that the plastids possessed by a plant are, as a rule, derived solely from the seed parent; the distribution of the chloroplasts in the pollen parent has therefore no influence upon the progeny, since no plastids from the pollen grains are brought into the egg-cell at fertilization. This is in contrast with the inheritance of characters carried by the nucleus, in respect of which the seedling receives heritage from both parents.

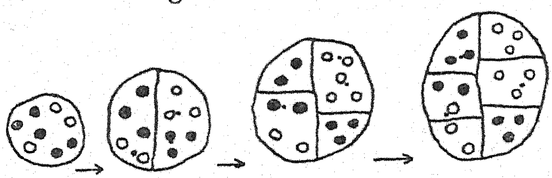


FIGURE 11

In some varieties of *Pelargonium* plastids from the pollen grain are contributed to the egg-cell at fertilization. On the left, an egg-cell containing chloroplasts (shown black) has received plastids incapable of developing chlorophyll from the pollen grain at fertilization. During the subsequent development of the fertilized egg-cell, regions become segregated containing *either* one *or* the other kind of plastid, the proportion of cells containing both kinds of plastids becoming so small as to be negligible.

(Exceptionally, plastids may be contributed from the pollen parent. In a species in which this happens, the offspring of a variegated plant are not necessarily uniformly green or uniformly colourless. Thus, if the second layer of the seed parent possesses chlorophyll-producing plastids and that of the pollen parent lacks them, the fertilized egg-cell will contain two kinds of plas-

tids, those present in the egg-cell able to develop chlorophyll and those contributed from the pollen grains unable to do so. During subsequent cell divisions by which the fertilized egg-cell develops into a seedling, these two kinds of plastids are separated from one another leading to the production of groups of cells that are either green or colourless—in other words, the seedling is irregularly variegated. How this separation of the two kinds of plastids during the early stages of development comes about is indicated in the diagrams on p. 49 (fig. 11).)

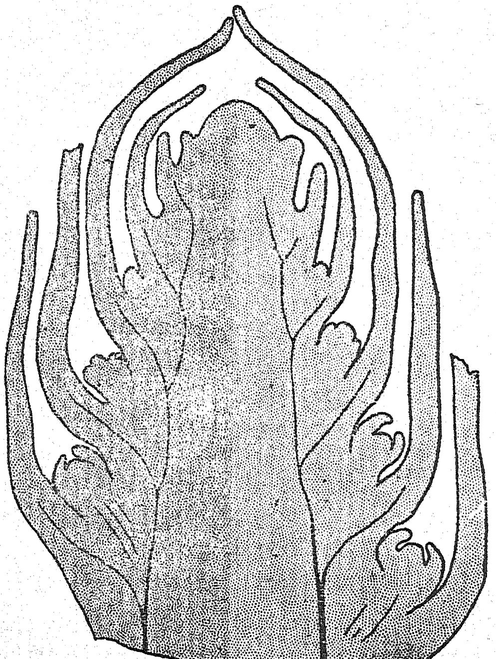


FIGURE 12

Median longitudinal section through the stem apex of a sectorial chimaera. If the more darkly stippled half of the tip represents dividing cells capable of giving rise to green tissues and the less darkly stippled half to cells that have not this capacity, then the mature shoot will bear green leaves on the left side and colourless leaves on the right.

Although the green and white patterns that characterize such variegated plants may be maintained almost indefinitely, a uniformly green or a uniformly colourless branch may sometimes arise spontaneously. The first may be explained as due

to the core tissues breaking through the skin—as may happen if the skin suffers mechanical abrasion or injury from an insect bite, the second to the origin of a lateral bud at a place where local thickening of the skin has occurred. The former occurrence might be expected to be the commoner, and observation shows that the production of wholly green branches from plants with white-margined leaves and of colourless branches from variegated plants with green-margined leaves is far more frequent than the converse.

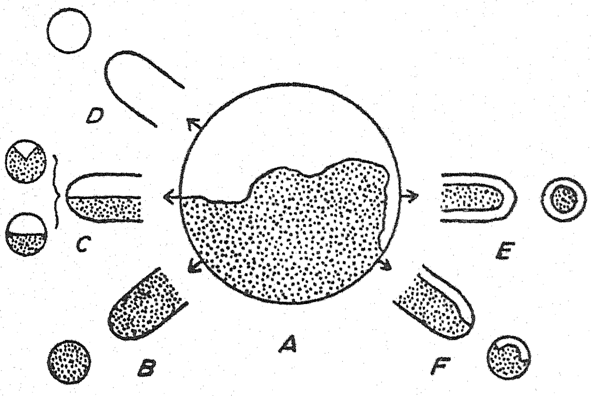


FIGURE 13

Diagram to explain the divergences from the sectorial pattern that may occur in the development of a shoot of a sectorial chimaera. Tissues containing chloroplasts are stippled. A, transverse section of the main shoot; B—F, lateral branches arising at different points. B, wholly green; C, sectorial chimaera; D, wholly white; E, periclinal chimaera; F, mericlinal chimaera. The only shoot reproducing the sectorial condition of the main shoot is C; the majority of lateral branches show a departure from this condition.

In the plant chimaeras so far considered the dissimilar tissues are arranged in a series of skins over a central core; these are called *periclinal chimaeras*. Another not infrequent arrangement is for one side of a plant or part of a plant to consist of one kind of tissue and the other side of another kind of tissue; these are known as *sectorial chimaeras* and arise from growing tips in which the tissues are arranged in the same side-by-side pattern (fig. 12). Whole plants or single branches in which one side is green and the other colourless are often seen in gardens.

A sectorial pattern is not usually long maintained by a shoot since lateral branches are either pure green, pure white, or tend to develop a periclinal structure; thus the sectorially arranged tissues soon become an insignificant part of the plant as a whole (figs. 13, 14).

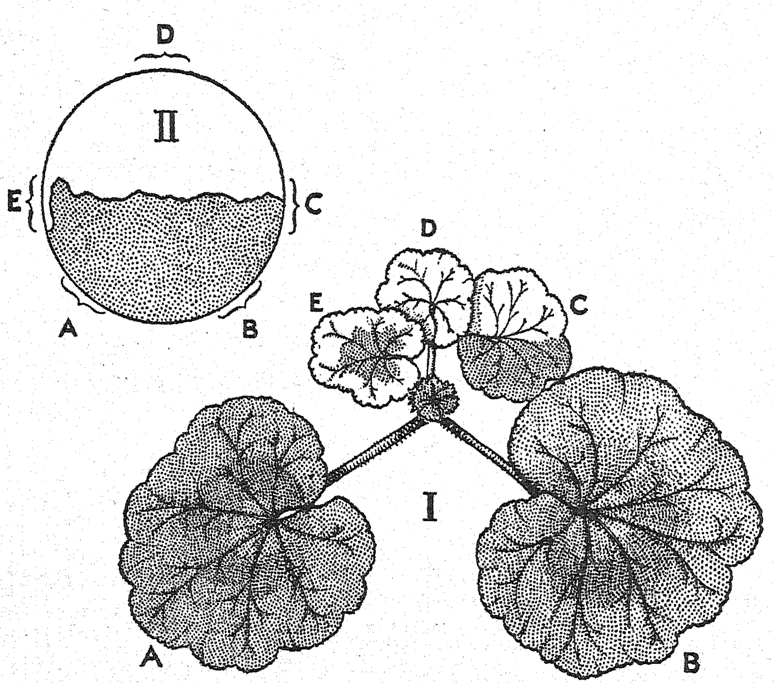


FIGURE 14

1. A young chimaeral plant of *Pelargonium* the main stem of which has a sectorial structure; looked at from above.
2. Transverse section through the main stem showing disposition of green and white tissues and the positions in which the five leaves shown in 1 originate.
A and B entirely green; D entirely white; C sectorial chimaera; E periclinal chimaera.

One of the surprising things about these periclinal chimaeras is the extent to which the various component skins and core may differ and yet succeed in behaving as a stable organic entity. Whilst combinations between varieties of a species are those most frequently met with of which the variegated plants just described form an example, combinations between two dif-

ferent species are not uncommon, while even those between different genera sometimes form a successful and stable unit.

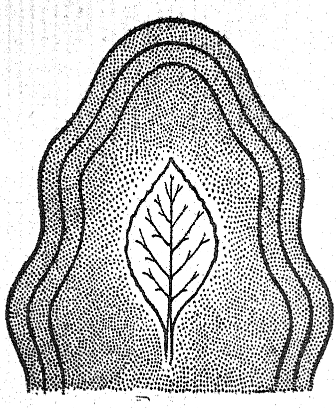
Thus, combinations between the two species Tomato and Nightshade were among the first plants to be recognized as having a chimaeral structure. In these, either one or two of the outer skins consist of Tomato (*Solanum Lycopersicum*), the rest of the growing apex consisting of Nightshade (*Solanum nigrum*); or the converse arrangements may occur (fig. 15). Each of the four types of growing tip gives rise to four kinds of plant distinguishable from one another in appearance but all intermediate between Tomato and Nightshade.

Those in which the core consists of Tomato tissue resemble Tomato more closely than Nightshade, and the reverse is true of those in which the core consists of Nightshade; this is to be expected since the bulk of the plant is derived from the core. On the other hand, superficial features such as the kind of hairs covering the plant and other epidermal characters, conform to those possessed by the species constituting the outermost skin; any seedlings resulting from self-pollination will be pure Tomato or pure Nightshade according to whether the second layer (from which the sex cells are derived) is composed of the former or latter species.

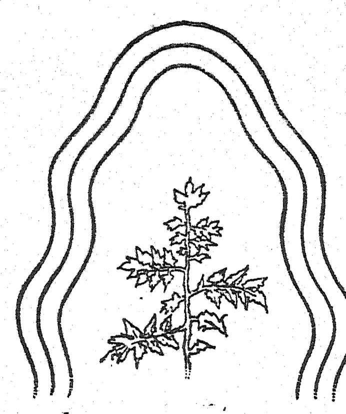
The production of these Tomato-Nightshade chimaeras is readily brought about by grafting one species on the other and cutting back the scion in the region of the junction after union is established. Buds arise from the cut surface a majority of which will grow into pure Tomato or pure Nightshade shoots, but a proportion will have a composite or chimaeral structure. The kind of shoot produced depends on the position of the bud in relation to the junction between the Tomato and Nightshade tissues as will be clear from the accompanying diagrams (fig. 16).

Another example of a chimaera of which the components are two different species is the remarkable plant known as *Cytisus Adami* (fig. 17). This, like the common Laburnum, has the habit of a small tree but the flowers are brownish instead of yellow; here and there branches arise bearing either yellow or purple flowers like those of the Laburnum or purple *Cytisus* respectively.

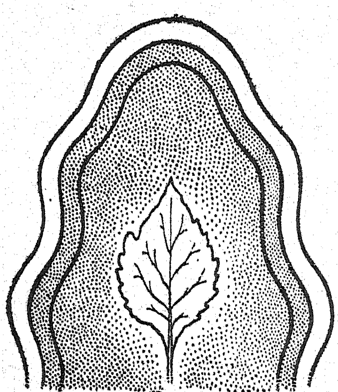
Cytisus Adami is believed to be a chimaera in which the central



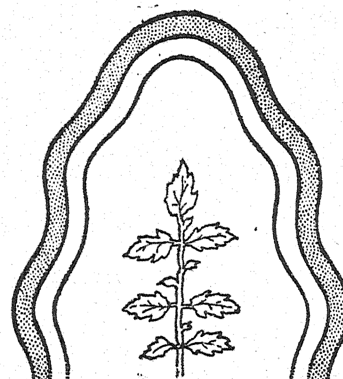
Solanum nigrum



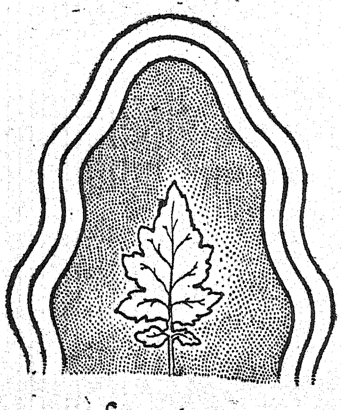
Solanum lycopersicum



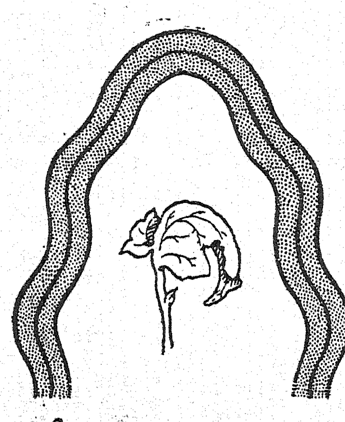
S. Tubingense



S. Koelreuteranum



S. proteus



S. Gaertnerianum

core consists of the common Laburnum (*Cytisus Laburnum*) and in which there is a single outer skin of the purple-flowered broom, *Cytisus purpureus*. The history of its origin is that a shoot of *C. purpureus* was grafted on a stock of Laburnum, a common horticultural practice when it is desired to obtain a 'standard' of the former species. In this case the scion failed to grow but at the junction of scion and stock a shoot arose that was neither *C. purpureus* nor Laburnum but showed some characters of each; cuttings from this shoot grew into plants subsequently named

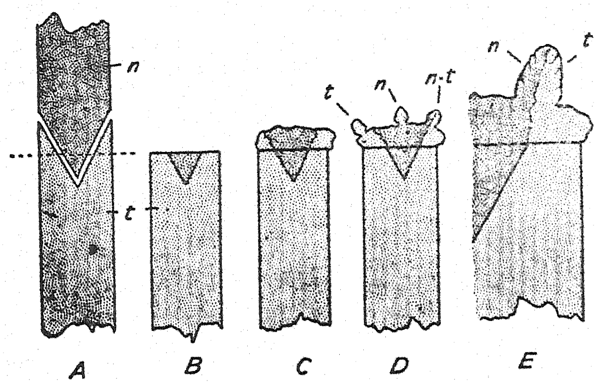


FIGURE 16

Diagram to illustrate the production of chimaeras by a grafting operation. A, nightshade (n) grafted on tomato (t); B, shoot cut transversely through the region of union; C, formation of callus over the cut surface derived partly from nightshade and partly from tomato; D, adventitious buds arising from the callus derived from tomato (t), from nightshade (n), and from the junction between the two (n-t); E, the bud (n-t) on a larger scale; its structure is that of a sectorial chimaera.

FIGURE 15 [see page 54

Diagrams of the growing apex of Nightshade (*Solanum nigrum*) and Tomato (*Solanum lycopersicum*) and of the derived periclinal chimaeras having one or two cell layers of one species enveloping the other.

Nightshade tissue stippled, Tomato tissue unshaded. Inset: leaf forms. Note that the leaf form resembles more nearly the species constituting the core. Some difficulty in adjusting growth rates appears to be inherent in the arrangement present in *S. Gaertnerianum* leading to leaf distortion.

Cytisus Adami. Because of its mode of origin the new plant was first regarded as a 'graft-hybrid', but from analogy with the way

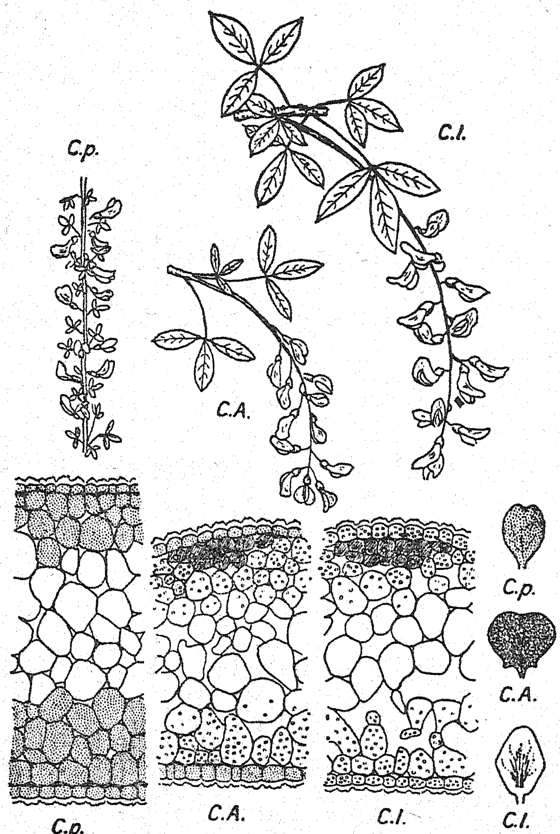


FIGURE 17

Cytisus Adami (C.A.) is a periclinal chimaera consisting of an epidermis of *C. purpureus* (C.p.) overlying a core of *C. Laburnum* (C.l.). The upper part of the figure shows the form of the inflorescence in these three plants; the bulk of the tissues of C.A. are derived from C.l. and the form of inflorescence in the two plants is very similar. The lower part of the figure shows transverse sections through the upper flower petal ('standard'); the epidermis of C.A. is seen to consist of cells containing a purple cell sap like that of C.p., while the rest of the tissue resembles that of C.l. (Fine stippling represents purple cell sap; scattered dotting yellow plastids; the group of thick-walled cross-hatched cells the brown 'honey guides' that occur only in the petals of C.A. and C.l.)

in which Tomato-Nightshade chimaeras are formed it is reasonable to assume that *C. Adami* is a chimaera compounded of Laburnum and *C. purpureus*. The latter interpretation is supported by the anatomical structure of the plant. For example, microscopic examination of the brownish-coloured petals of *C. Adami* shows that the cells of the outermost layer or epidermis contain a purple cell sap as does *C. purpureus*, while the deeper-lying cells contain yellow plastids as does Laburnum, the purple overlaying the yellow giving a brown coloration. The types of hairs on the plant are similar to those of *C. purpureus* and different from those found in Laburnum. The various reproductive peculiarities described for variegated plands and possessed in common with other similar chimaeras are shown by *C. Adami*. Thus, *C. Adami* gives rise to pure Laburnum when propagated from root cuttings; on the rare occasions when it has produced fertile seed, the seedlings have always been pure Laburnum in conformity with the supposition that the second layer consists of Laburnum tissue; and the occasional production of branches of pure Laburnum or pure *C. purpureus* spontaneously from the stem is analogous to the behaviour of variegated plants and similar chimaeras. There is, however, the surprising fact that no one has ever succeeded in producing *C. Adami* again by grafting or in any other way; all the plants now in existence have been derived from the original shoot of *C. Adami* produced by vegetative propagation in 1825 by M. Adam, in his horticultural nursery near Paris.

As examples of the rare cases in which two different genera are combined may be mentioned the chimaeras artificially derived from Medlar (*Mespilus germanica*) and Hawthorn (*Crataegus monogyna*) (fig. 18), and between Pear (*Pyrus communis*) and Quince (*Cydonia vulgaris*), all obtained as a result of grafting one plant on the other and consisting of a skin of Medlar or Pear enclosing a core of Hawthorn or Quince respectively.

Chimaeras of this type with a skin of one kind of plant over a core of another show great stability in retaining the particular pattern of their composite structure. Obviously such plants may furnish a means of tracing the contributions made by any zone towards the mature tissues of the plant, provided the cells of

the zone in question are recognizably different from those constituting the rest of the growing tip.

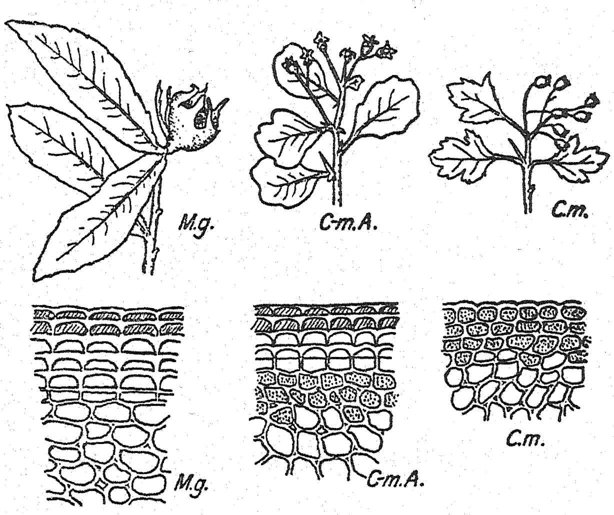


FIGURE 18

The periclinal chimaera *Crataego-mespilus Asniersii* (C-m.A.) and its two components *Mespilus germanica*, the Medlar (M.g.), and *Crataegus monogyna*, Hawthorn (C.m.). The epidermis of the fruit in Medlar produces several layers of cork to which the brown colour of the fruit is due; the epidermis and several more deeply seated layers in Hawthorn contain a red cell sap; the fruit of C-m.A. has a superficial covering of cork beneath which is a zone of cells with red cell sap. These fruit characters suggest that C-m.A. consists of a core of Hawthorn with an epidermis derived from Medlar; other characters of the plant support this interpretation.

Although chimaeras may result from a grafting operation under artificial conditions of culture, it is unlikely that those met with in nature have originated in this manner. The most obvious way in which the latter could arise is by the occurrence of a spontaneous change or 'mutation' in a cell, or possibly a group of cells, in some localized region of the growing apex. Such sudden changes, depending on some abnormality in nuclear division, are relatively rare, and it is unlikely that all the cells composing the growing apex will be affected similarly. It is not surprising, therefore, that the 'bud sports' or 'vegetative

mutations' that arise from time to time in nature almost invariably possess a composite or chimaeral structure.

It may be noted that the existence of such chimaeras as the foregoing in ferns and other lowly plants is impossible since the stem apex possesses only a *single* dividing cell from which *all* the mature tissues are derived (fig. 7, p. 42).

Although possession of variegated foliage, especially when it takes the form of a difference in the leaf margin, can usually be ascribed to the fact that the plants concerned have a chimaeral structure, it must not be assumed that *all* variegation is of this nature; there are at least two other causes that may lead to such a result.

Hereditary variegation

A variegated pattern may be inherited due to the passing on from parent to offspring of a pattern-producing hereditary factor or gene, carried by the nucleus and inherited according to Mendelian rules like those that govern leaf shape, stature, or other varietal characters.

Hereditary variegation of this kind is somewhat rare; as an example may be cited those varieties of 'Garden Nasturtium' (*Tropaeolum major* and *T. minor*) having a fine green-and-white mosaic pattern in the leaves.[1]

In contrast with the rarity of inheritance of a special kind of variegation in leaves by the passing on of hereditary factors or genes from parent to offspring, the existence of 'pattern genes' controlling the distribution of colour in the petals of flowers is of common occurrence. Examples are the purple spots of Foxglove flowers, the coloured edge of 'picotee' carnations or that of the petals of Shirley poppies, all of which patterns are inherited in the same way as any other Mendelian character.

Infective variegation—Virus diseases

Another, and unfortunately more common, cause of leaf variegation is infection of the plant by a virus disease. The ailments

[1] The varieties known horticulturally as '*albopulverulea*'.

from which plants suffer may be regarded broadly as being due to three different kinds of provoking cause. In the first place there are what are known as physiological disorders due to such causes as deficiency of some necessary nutrient, the presence of some deleterious substance, or to some physical condition of the environment that renders it unsuitable for plant growth. The cause lies in the nature of the environment and however severe the symptoms healthy plants are in no danger of contact infection.

Then there are diseases the symptoms of which are caused by attack by some parasite such as a fungus or bacterium; such diseases are infections since the parasite can spread from a diseased to a healthy plant. To what extent the disease will spread in fact depends on how favourable the conditions are for dissemination of the attacking organism and how susceptible the healthy plant is to attack, the latter depending on the variety or species of plant and on its condition of health at the time. The nature of the disease can be diagnosed from the symptoms produced in the host plant and the organism responsible can be detected by microscopic examination of the attacked tissues. Confirmation of the diagnosis can usually be obtained by isolation of the parasite, its cultivation on a synthetic medium, and the reappearance of the characteristic disease symptoms when the organism is brought into contact with a healthy host plant.

Finally, there are a number of infective diseases in which no causal agent can be detected microscopically. These are the so-called virus diseases, the infective agent being known as a virus. In addition to the fact that they are ultramicroscopic, many infectious viruses are able to pass through filters that arrest the passage of the smallest bacterial cell. None has hitherto proved capable of multiplication except in living cells. Certain infective diseases of animals—measles, smallpox, foot-and-mouth disease of cattle—are caused by infective viruses having similar characters.

It was first suggested that viruses might be organisms far smaller than any known bacteria, below the size of objects that can be seen under the microscope. Examination by X-rays and the electron microscope have confirmed the small size of virus

particles and shown that they vary in shape from spherical particles to long threads. The extreme smallness of the particles raised doubts as to whether the sort of organization associated with a living cell was possible in so small a compass. This doubt was strengthened by chemical investigations which showed that viruses contain only two essential constituents, nucleic acid and protein, a chemical simplicity that separates them sharply from even the simplest organisms. Added to this, many viruses have been obtained in a purified form as crystals. All these facts have led to the belief that viruses are not living organisms as ordinarily understood, but rather non-living proteins of a special kind having the power of self-propagation when introduced into an appropriate living cell. They may be regarded, in fact, as forming a link between living and non-living matter in respect to their organization.

One of the common symptoms of infection by a virus disease is localized failure of chlorophyll production; this condition is usually accompanied by more or less serious ill health, often leading to the ultimate death of the affected plant. Occasionally, however, whilst causing marked variegation of the foliage, a virus infection may lower the general health of the plant only slightly. Such virus-infected plants have been deliberately cultivated for the sake of the mottled foliage they produce. A well-known example is the plant passing under the name of *Abutilon Thompsoni*. Actually this is a diseased form of *Abutilon striatum* suffering from a virus infection which reduces only slightly its vigour of growth and of which the mottled foliage is one of the symptoms.

It is of interest to note that infection by virus diseases sometimes produces analogous effects in the development of flower colour; instead of a mottling of the foliage, or in addition to it, virus infection may be indicated by local failure of colour production in the petals with the result that the flowers are striped instead of uniformly coloured. Examples of such striped flowers are common among Tulips (fig. 19), Wallflowers, and other garden plants; they can often be recognized by the irregularity and radial arrangement of the pattern in contrast with the usually well-defined limits and concentric arrangement of colour

markings when these are due to inheritance of a special pattern gene.

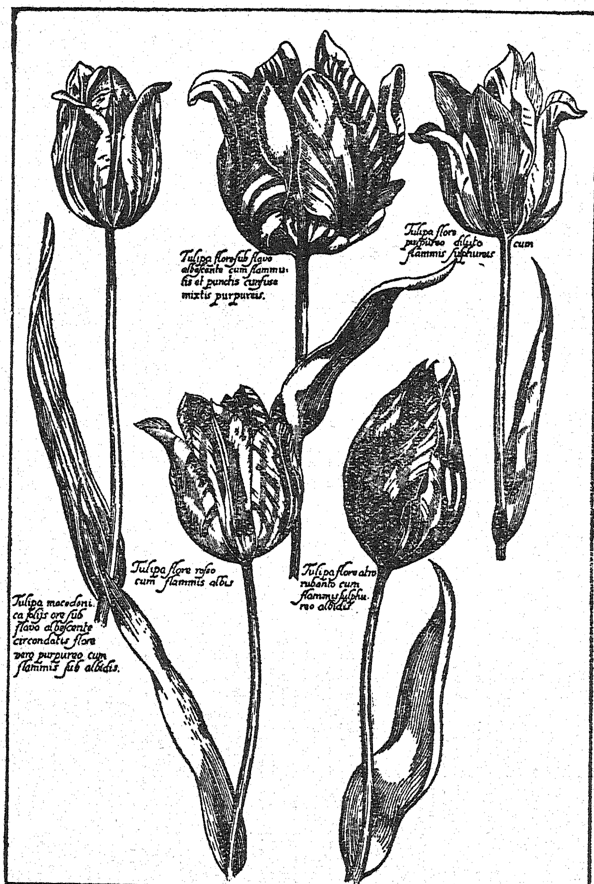


FIGURE 19

Examples of striped or 'broken' tulips in which the pattern is due to local failure of production of pigment as a consequence of infection by a virus disease.

When, as occurs in the case of Tulips, the general health of the plants is not too seriously lowered, virus-infected individuals bearing striped flowers of such origin may find their way on to the horticultural market under special varietal names as in the case of *Abutilon Thompsoni*. Thus, for almost every self-coloured

garden variety of Tulip there is, under another name, a corresponding striped variety that consists of the former carrying a virus infection. These striped, or 'broken', forms are invariably less vigorous than the self-coloured uninfected stock from which they are derived, although the loss of vigour is insufficient to preclude their ready cultivation. Illustrations dating from the beginning of the seventeenth century show that 'broken' forms appeared early in the cultivation of the garden Tulip; in fact, the older florists valued the broken flowers far more than the self-colours, a preference that persisted to the late nineteenth century. Time has seen a complete reversal of this judgment and such change may be welcomed, since one cannot but feel that approbation of the disease symptoms shown by the flowers of these 'broken' Tulips, or by the leaves of plants like *Abutilon Thompsoni*, even though the disease is not crippling, has something unwholesome about it—like admiring a pallid and delicate complexion due to ill health.

In far and away the greater number of garden plants with variegated foliage, however, variegation is due neither to the presence of an inheritable pattern-determining gene carried by the nucleus, nor to infection by a virus disease, but depends on the special make-up of the growing point characteristic of a plant chimaera, in which certain layers of the actively dividing growing point do and others do not consist of cells containing plastids with the ability to form the green pigment chlorophyll. Should an aesthetic appeal be exercised by these plants, the reader need feel no hesitancy, therefore, in its indulgence on the score that pleasure is being derived from a symptom of disease.

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(The first and third references are short, simple but comprehensive accounts of the phenomena concerned; the second deals with some aspects of chimaeras within the scope of a single lecture; the last is an advanced work.)

Chapter 3

PLANT RESPONSES AND PLANT HORMONES

The shoot of a flowering plant may be regarded as made up of three regions in respect to growth processes. At the extreme tip there is the cone-shaped mass of actively dividing small cells, a fraction of an inch in length, known as the *apical meristem*. Behind this is a zone of elongation, an inch to several inches long; here the newly formed cells increase in size, especially in a longitudinal direction, mainly in consequence of absorbing large quantities of water. Still farther from the tip the fully elongated cells become modified or *differentiated*, that is, the cell walls and contents undergo changes that convert them into the different kinds of specialized cells or units that make up the tissues of the mature stem.

It must not be supposed that these three regions are sharply marked off from one another; on the contrary, one merges into the other, cells that are still undergoing division, for instance, occurring amongst others that have ceased to divide but have begun to absorb water and elongate. None the less, it remains broadly true that the three kinds of cell activity referred to—division, enlargement, differentiation—predominate successively as one passes backwards from the apex to the mature part of the stem.

The present chapter is concerned mainly with the behaviour of the second region, that of elongation, and a question that immediately presents itself is why elongation of the stem should take place.

Growth Hormones

As is generally known, the higher animals possess special organs, the so-called ductless glands—thyroid, pituitary, adrenal, and so forth—the secretions from which, distributed all over the body in the bloodstream, may affect the functioning of organs far distant from the glands that produce them. These secretions are given the general name of *hormones*: each has a definite chemical composition and a specific effect on the functioning of some particular organ; they may be regarded as 'chemical messengers' sent from the glands to control the functioning of some distant part of the organism.

Only after the existence of hormones and their controlling action in animals had come to be generally accepted was it realized that a parallel if less elaborately organized system of control occurs in plants. Of plant hormones the best known are the substances called *auxins*, produced notably in the stem tips of the higher plants, whose action on stem tissues some distance away justifies the title of 'growth hormones'. As will be described presently, these auxins pass from the tip downwards through the living cells and induce enlargement of the cells situated in the region of elongation.

Plant Auxins

The existence in plants of substances controlling growth was foreshadowed so long ago as 1880 when the German botanist Sachs put forward the idea that the development of different organs by a plant during growth was the result of the local concentration of definite and specific organ-forming substances, although the same thought had been in the minds of various workers before his time. Sachs offered no experimental support for his hypothesis. In the same year Charles Darwin made the suggestive discovery that when the extreme tip is removed from a root, the root loses its power of responding to gravity by a downward curvature when placed in a horizontal position.

From this behaviour he deduced that the tip acts as a 'perceptive' organ and that when in a horizontal position a stimulus is transmitted from it to a region some distance away where a curvature is induced which brings the 'perceptive' tip into a vertical, unstimulated, position. Unfortunately, Sachs's hypothesis regarding the occurrence of organ-forming substances did not suggest to Darwin, nor did Darwin's experiments suggest to Sachs, that the 'stimulus' transmitted from the 'perceptive' to the 'reacting' region might be in actual fact a concrete substance transported through the intervening tissues.

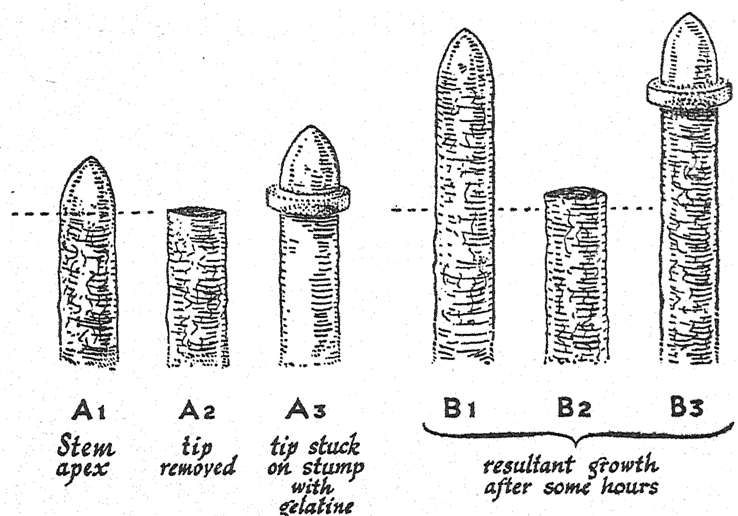


FIGURE 20

Experiment showing that stem elongation virtually ceases when the tip is removed, but continues if the tip is replaced although separated from the stem by a disc of gelatine. Interpretation: stem elongation is due to auxin derived from the tip, and the auxin can diffuse through a non-living barrier of gelatine.

The interest of botanists in the possibility that control of growth processes in plants might be exercised by chemical substances was awakened by the discovery of animal hormones by Bayliss and Starling in 1904, but the first clear demonstration that a parallel mechanism existed in plants was not obtained until some ten years later, when it was shown that elongation of

a shoot growing vertically not only ceases when the tip is removed, but that growth recommences if the excised tip is stuck in its original position upon the decapitated stem with a little warm melted gelatine. Such an experiment shows that some substance controlling stem elongation, now called an *auxin*, is derived from the tip, and also that this substance can diffuse through a gelatine film uniting the excised tip with the stump of the stem (fig. 20).

Collection of auxin and measurement of its concentration

Further experiment showed that if an excised stem tip is placed on a small square of moist gelatine, the auxin diffuses out of the tip and accumulates in the gelatine; consequently, when a square of gelatine film so treated for a few hours is

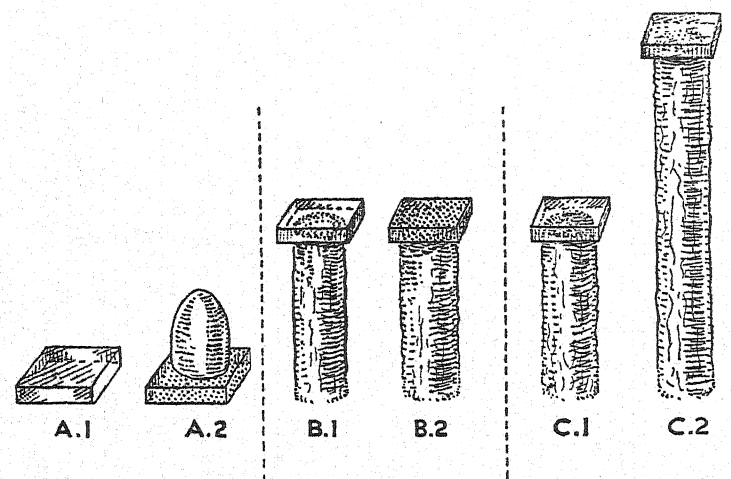


FIGURE 21

Experiment showing that auxin collects in a block of gelatine if an excised stem tip is placed upon it (A.1., A.2.). If a gelatine block containing auxin is placed on the decapitated stem, the auxin diffuses into the stem causing elongation (B.2., C.2.) which does not happen when the block does not contain auxin (B.1., C.1.).

The presence of auxin in the block is indicated by stippling.

applied to the end of a decapitated stem, the auxin diffuses from the gelatine and brings about elongation of the stem as happens when the tip is similarly applied (fig. 21). There is, of course, an important difference in persistence of the effect in the two cases. That of the latter lasts so long as the tip is alive and continues to produce fresh supplies of auxin; that of the former ceases when the supply of auxin originally present has diffused out of the block, and a new block of gelatine containing fresh supplies of auxin must then be substituted if elongation is to be maintained.

The concentration of auxin in a gelatine block can be built up to a high value if a number of freshly excised stem tips are placed successively on the same block, each for three or four hours. Such a block when applied to a decapitated stem may bring about elongation to a greater extent than that normally occurring in the intact seedling.

Careful measurements show that the amount of elongation taking place in a stem bears a direct relation to the concentration of auxin in the block. This relationship is of considerable practical interest when it is desired to make comparative measurements of the concentration of auxin present. Direct measurements by chemical estimation are extremely troublesome if only because the concentrations concerned may be of the order of a few parts per million; measurements of stem elongation on the other hand are readily carried out.

An even more convenient and sensitive method for determining auxin concentration is to measure the curvature that follows when the gelatine block containing auxin is applied eccentrically so as to be in contact with one side only of the top surface of the decapitated stem (fig. 22).

Experiment has shown that transport of auxin in the stem is strictly longitudinal; consequently, diffusion occurs only down the side to which the block is applied and elongation is confined to this side. The result is a curvature away from the side carrying the gelatine block. The extent of the curvature depends on the degree of elongation taking place, this in turn being directly related to the concentration of auxin diffusing from the gelatine block. Up to about 20° deviation, the angle of curvature pro-

duced has been found to be directly proportional to the concentration of the auxin. Thus, if a gelatine block applied to a decapitated stem under standard conditions produces a curvature of 5° and another block of the same size applied to a similar

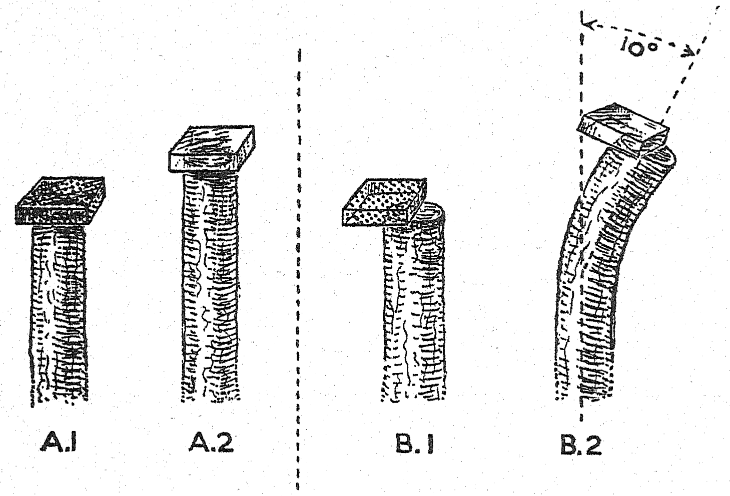


FIGURE 22

Experiment showing that auxin diffuses from a block of gelatine containing it when this is placed on a decapitated stem, so causing elongation (A.1., A.2.); if such a block is placed on one side of the stem, elongation occurs on that side only so that a curvature is produced. The experiment also shows that auxin diffuses through the living tissues of the stem in a longitudinal direction only and that lateral diffusion does not occur.
The presence of auxin in the block is indicated by stippling.

stem produces a curvature of 10° it may be concluded that the concentration of auxin in the latter was double that in the former. It is obvious that if satisfactory comparative results are to be obtained, all the conditions must be carefully standardized.[1]

[1] For example, F. W. Went, one of the pioneers in this line of research, raised oat seedlings in darkness, at a temperature of 25° C. and 90° humidity, decapitated them when 30 to 40 mm. long, and after forty minutes applied blocks of agar 2 × 2 × 1 mm. containing auxin to one side of the stumps. A concentration that produced a curvature of 1° after two hours was adopted as one unit of auxin. Other workers adopted different units; for example,

If an auxin solution of known concentration is available, it may be used to determine the strength of any other solution in the following simple way that avoids the necessity for elaborate standardization of the living material.

A number of pea seedlings are raised, preferably in the dark, and the ends of the shoots cut off to a length of about 6 cm. ($2\frac{1}{2}$ inches). Each shoot is split by a vertical cut from the tip downwards for a distance of 2 to 3 cm. ($\frac{3}{4}$ to $1\frac{1}{4}$ inches). If one of these split shoots is immersed in water, the split halves will be found to curl away from one another, attaining a stable position in about two hours (fig. 23A). If the water contains auxin, however, the split halves curl *towards* one another, the degree of

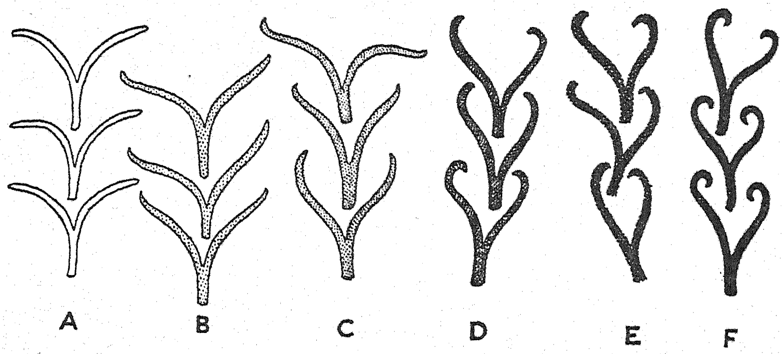


FIGURE 23

Measurement of auxin concentration. If split pea shoots are placed in water, the split halves curl away from one another (A); if placed in a solution containing auxin they curl towards one another, the degree of curvature increasing with increasing concentration of the auxin (B–F).

inward curvature increasing with increase in strength of the auxin solution (fig. 23:B–F). To find the strength of the unknown solution of auxin, the degree of curvature produced in one of the split shoots when immersed in it is determined, after which

Kögl chose as a unit the amount of auxin in a block of 2 × 2 × 0·5 mm. that caused a curvature of 10° under specified standard conditions. Knowing the standard conditions employed, it is possible to correlate the different arbitrary 'units' used by different workers. Instead of using these comparative units it is now usual to express concentration of auxin in terms of absolute concentrations of synthetic heteroauxin (p. 72).

the degree of dilution of the known solution needed to produce the same degree of curvature is ascertained, from which the concentration of the unknown solution can be calculated. (If the unknown solution has a higher concentration than the known solution, dilution of the former instead of the latter will be required.)

The chemical nature of auxins

The fact that the auxin produced by an excised stem tip passes downwards and diffuses from the lower cut surface enables it to be collected in sufficient amount to be identified chemically. From chemical analyses it appears that two substances of allied constitution are concerned, both of them acids, known to botanists as *auxin-a* and *auxin-b* respectively.[1] These two substances are characteristic products of the higher plants, formed in regions such as stem growing points and young leaves; they are found also in other tissues as the result of transportation. The effects produced by them are identical in kind and degree.

Many lower plants, especially certain fungi, produce a substance with similar properties in controlling growth in the higher plants, but having a different and much simpler chemical structure. This substance is called *heteroauxin* and is identical with the compound known chemically as indole-3-acetic acid.[2] Besides being a characteristic product of fungal activity, heteroauxin occurs in many animal tissues and also in secretions of the animal body such as saliva and urine, especially in the urine of vertebrate animals fed on diets containing certain kinds of fat.[3] Although behaving towards the higher plants as a highly active

[1] How closely they are related is indicated by the fact that the former has a formula $C_{18}H_{32}O_5$ and a molecular weight of 328, the latter a formula $C_{18}H_{30}O_4$ and molecular weight of 310.

[2] Heteroauxin has a formula $C_{10}H_9O_2N$, and a molecular weight of only 175.

[3] For example, fats such as olive oil and butter that contain tryptophane, but not hydrogenated coco-butter which does not. Tryptophane itself is inactive but is an indole compound (indole-3-alamine); organisms appear capable of converting this into active indole-3-acetic acid.

growth hormone, it does not appear to exercise any obvious control on the growth of the organisms that produce it.

These three substances, auxin-a, auxin-b, and heteroauxin, are indistinguishable in physiological action, all inducing in Flowering Plants elongation of the stem and other kinds of growth control when present in concentrations as low as a few parts per million. They have about the same activity at similar concentrations, but may be distinguished readily by their differing degrees of stability, thus:

Auxin-a is stable towards acids, but destroyed by alkalis.

Auxin-b is destroyed by acids, and destroyed by alkalis.

Heteroauxin is destroyed by acids, but stable towards alkalis.

Of the auxin present in stem tips, auxin-a appears to constitute the main part, auxin-b only a minor part, neither being found in fungi or in animals; on the other hand, heteroauxin is formed in considerable quantities by many fungi and occurs also in animal tissues and excretions, but is not formed by higher plants.

Unlike the two auxins, heteroauxin can be readily synthesized by chemists in the laboratory and so obtained pure in unlimited quantities. As a consequence, the majority of experimenters investigating the action of growth hormones in plants have used synthetic heteroauxin; the physiological effects are the same as those of the naturally occurring auxins and heteroauxin, laborious extraction from living tissues is not called for, and solutions of known concentration are easily prepared. Concentrations of growth-controlling substance are now generally expressed in terms of the amounts of synthetic heteroauxin required to produce like effects instead of in arbitrary units.

To the question asked at the beginning of this chapter we can therefore reply that the stem elongates in response to stimulation produced by a growth hormone or auxin formed by the cells of the growing apex. But this answer only goes part of the way towards a complete explanation. We want to know, for example, why the presence of the auxin should bring about extension of the newly formed cells.

Mode of action of auxins

With the exception of the dividing cells at the extreme tip, every living cell of the shoot is a closed protoplasmic bag containing a central space or *vacuole* filled with liquid and surrounded by a non-living cell wall. Enlargement of a cell under the influence of auxin might be brought about in two ways: there might be an increase in the internal pressure by absorption of additional water into the vacuole, so stretching the cell wall, or there might be some alteration in the cell wall whereby this becomes more easily stretched in which case the existing internal pressure would suffice to bring about cell distension; or there might be a combination of these two causes. There is reason to believe that the second of these possibilities is the one realized, that the action of the auxin is mainly if not solely on the cell-wall which is rendered more plastic and therefore more readily stretched. In support of this view there is evidence that the walls of dead cells are affected similarly by auxin.[1]

Transport of auxin

Another point of interest is the manner in which auxin moves from its place of origin in the stem tip to the region of elongation. As might be expected in the absence of a bloodstream, transport of auxins in plants is far slower than is that of hormones in animals; on the other hand, it is more rapid than can be accounted for by simple diffusion, suggesting that streaming movements of the living protoplasm, a phenomenon frequently to be observed in living cells, may be concerned.

One of the most surprising facts about transport of auxins is that movement through living plant tissues takes place in one direction only; namely, from the tip downwards to the more basal regions. As a consequence, there is brought about a gradient of increasing concentration from apex to base of a

[1] Robbins, W. J. and Jackson, J. R. 'Effect of 3-indole acetic acid on cell walls of stem and root.' *Am. Jour. Bot.*, *24*, 83, 1937.

shoot. Movement of a substance in solution, when due to diffusion, is always from a region of greater to one of less concentration; movement of auxin downwards through the living tissues of a stem is in the contrary direction, against the diffusion gradient instead of with it. A movement of this kind calls for expenditure of energy. This is another indication that living matter plays some part in the movement of auxin, providing in some way the energy that enables this movement to occur in opposition to the purely physical process of diffusion.

The movement of auxin through the stem in one direction

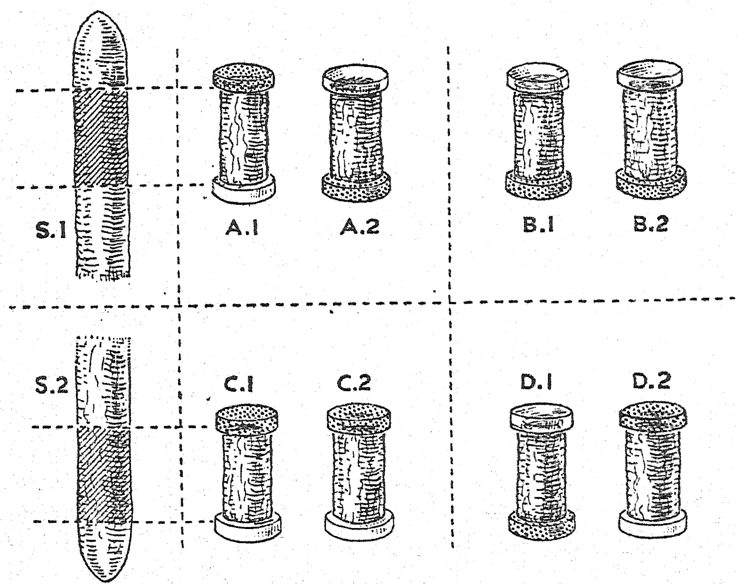


FIGURE 24

Experiment to demonstrate that auxin is transported through the living tissues of the stem in an apex-to-base direction only. Gelatine discs are applied to the ends of a short piece of young stem; the upper disc contains auxin (A.1.). After some hours the whole of the auxin is transferred to the lower disc (A.2.). If the disc containing auxin is applied to the lower end of the piece of stem (B.1.), no transmission of auxin through the stem is observed (B.2.).

That gravity is not concerned in determining the direction of transport is shown by the experiment illustrated in C.1., C.2.; D.1., D.2. in which the piece of stem is inverted (S.2.).

only can be demonstrated by very simple experiments such as those illustrated in fig. 24: A1, A2, B1, B2. Two gelatine blocks are placed in contact with the ends of a short length cut from the stem of a suitable seedling. The condition at the beginning of the experiment is shown in A1, in which the block at the apical end, as indicated by the stippling, contains a supply of auxin whilst that at the other end does not. A2 shows the auxin distribution after some hours, the whole of the auxin having been transferred from the apical to the basal block, provided that sufficient time has been allowed for the transference. Fig. 24, B1, shows the experiment repeated with the positions of the two blocks reversed; in this case there is no transference of auxin (B2), proving that movement of auxin in the opposite direction through the shoot does not take place. That gravity is not concerned in any way with producing this result can be shown by performing the experiment with a piece of stem in the reversed position (fig. 24: C1, C2, D1, D2).

Growth curvatures

Gravity and light behave as definite stimuli to the growth of plant organs, causing curvatures that bring about changes in the direction of growth. These reactions have always excited the interest of botanists. It is now realized that the mechanism whereby such curvatures are produced is concerned mainly with unequal auxin distribution.

Under the stimulus of gravity, a stem placed in a horizontal position grows more rapidly on the lower than on the upper side, thus bringing the stem eventually into a vertical position; when illuminated unequally on the two sides, a shoot grows more rapidly on the side receiving less light with the result that the stem bends towards the brighter light. Such behaviour would follow if production of auxin by the stem apex were greater on one side than on the other, since one side of the region of extension would then receive more auxin than the other owing to transport of auxin being strictly longitudinal.

That this unequal production of auxin by the two sides of the

stem apex actually does occur under the stimulus of gravity or light can be proved by the experiments illustrated in fig. 25.

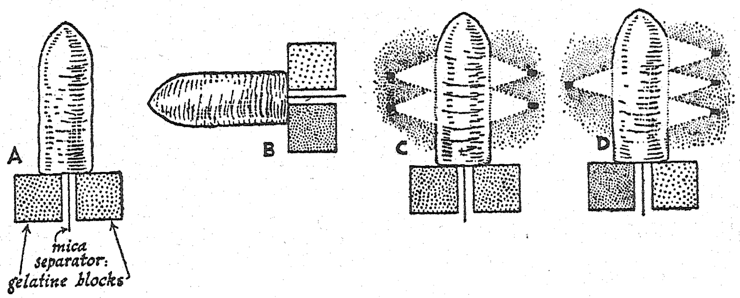


FIGURE 25

Experiment to show the effects of gravity and light on production of auxin by a stem tip.
A—An excised stem tip is placed vertically on two blocks of gelatine separated by a sheet of mica to prevent lateral diffusion. As indicated by the stippling, equal amounts of auxin accumulate in the two blocks, so providing evidence of a uniform production of auxin by the tip. *B*—A similar experiment except that the tip is in a horizontal position. In this case more auxin accumulates in the lower block, suggesting a movement of auxin to the lower side of the tip. Had the tip been attached to a stem, the lower side of the stem would have elongated more than the upper side, causing a curvature that would have brought the tip into a vertical position. *C* and *D* illustrate how the production of auxin is affected when the tip is illuminated equally and unequally on the two sides.

Two similar gelatine blocks placed side by side are separated by a thin sheet of mica so that diffusion cannot take place from one to the other. In contact with the blocks is a freshly excised stem tip arranged in such a way that the auxin derived from one half of the tip diffuses into one block and that from the other half into the other. If, with the tip in a vertical position, the two blocks are tested after three or four hours for the relative amounts of auxin they have accumulated from the two halves of the tip, it will be found that the auxin content of each block is the same (fig. 25, A); if the tip is in a horizontal position throughout the experiment, one block being vertically above the other, then nearly the whole of the auxin will have diffused into the lower block (fig. 25, B). From this it may be concluded that

when a stem is placed in a horizontal position there is a greater production of auxin from the lower side of the tip with the result that the lower side of the stem elongates more than the upper, causing a curvature that brings the stem into a vertical position.

An experiment of a similar kind in which two stem tips are vertical, one illuminated equally on all sides and the other unequally on opposite sides, would show in the case of the latter that more auxin is produced from the side exposed to the weaker light (fig. 25, C and D). Consequently, the side of the stem facing the weaker light receives more auxin and elongates to a greater extent, causing a curvature towards the source of stronger illumination.

Growth curvatures taking place under the influence of gravity and light may be attributed therefore to unequal production of auxin by the two sides of the tip, the so-called 'perceptive' region, leading to unequal distribution of auxin towards the two sides of the curving or 'reacting' region.

If we wish to push the inquiry further and ask how stimuli such as those of gravity and light are able to disturb the normal uniform production of auxin by the stem tip, we enter upon controversial issues the adequate treatment of which would take us beyond the limits possible in the present discussion. It may be said, however, that so far as the stimulus of gravity is concerned, the total amount of auxin produced is unaltered by the stimulus. The effects observed when the stem tip is horizontal would be explained if the auxin were able to move laterally to the lower side of the tip under the influence of gravity, although, as we have seen, movement can occur only longitudinally in *mature* living tissues. In the case of growth curvatures produced by unequal illumination on two sides of an organ, the effect of light on the auxin is more complex and may involve inactivation as well as redistribution. That exposure to light causes inactivation of auxin is borne out by the well-known fact that the stems of plants tend to elongate in weak light, while elongation may be greatly curtailed under intense illumination. The rosette habit of many alpine plants in nature is a good example of behaviour due to the latter cause and may be greatly modified if they are grown in a dull light. Those who wish to pursue the

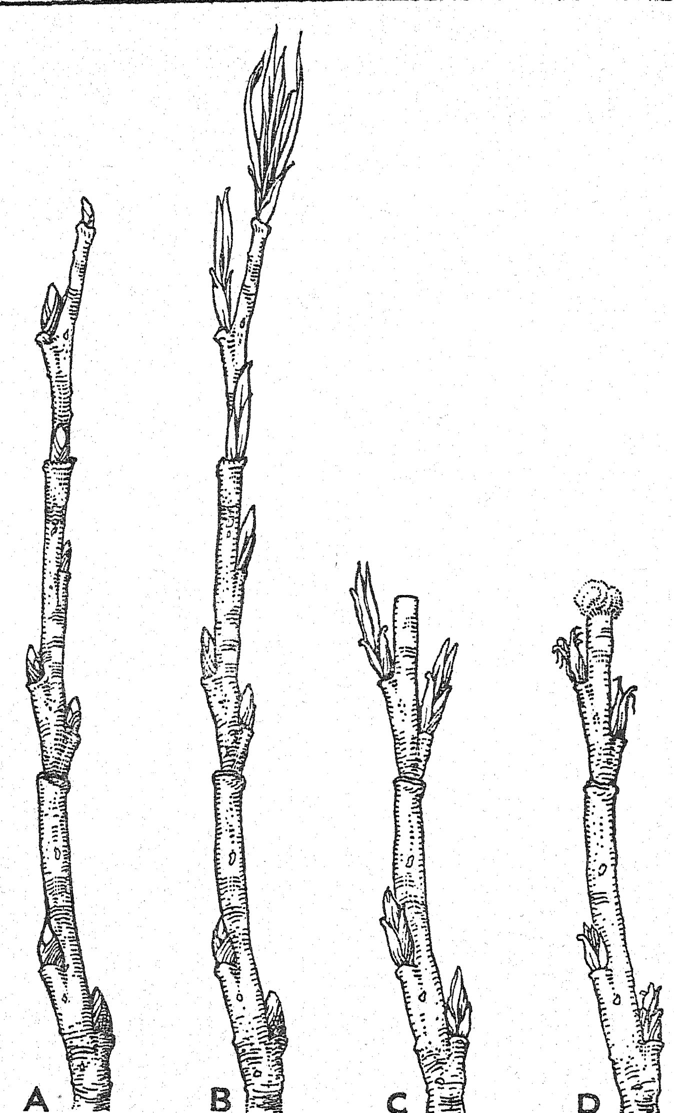
matter further must refer to the specialist literature on the subject.

The control of bud development

Control of cell extension is only one of the many roles played by auxins; there is, for example, their effect in suppressing the development of growing regions such as those of lateral buds.

Everyone who has pruned rose bushes or fruit trees knows that the lateral buds on a shoot do not all develop equally: the tendency to grow out is greatest at or near the stem apex, decreasing towards the base of the shoot where many buds usually remain quiescent (fig. 26, B). These dormant buds can be made to develop by cutting off the part of the shoot above them, suggesting, what is indeed the fact, that the buds nearer the apex curtail the development of those nearer the base (fig. 26, C).

This behaviour becomes intelligible if we correlate two facts: one, that owing to one-way transport, an auxin gradient is established in the stem with concentration greatest at the base; the other, that inhibition of lateral bud development is exercised by auxin in proportion to its concentration. The progressive loss of vigour of growth from apex to base on the part of the lateral buds is a reflexion of the gradient in auxin concentration within the shoot. Cutting back a shoot, as in pruning, removes the source of auxin production in the more apical buds, so that transport from above no longer brings about a high concentration of auxin towards the base of the shoot and the growth of lateral buds in this region is no longer inhibited. That failure of the lower buds on a shoot to develop is really due to the inhibiting effect of auxin can be shown by smearing the cut end of a branch after pruning with lanolin containing a little heteroauxin. After such treatment, the lateral buds immediately below the cut do not start into growth as happens usually after pruning (fig. 26, D); the heteroauxin entering the stem from the lanoline acts in the same way as the auxin derived from the apical buds of the intact shoot, suppressing the development of any lateral buds it reaches in sufficient amount. One must



A — *Woody shoot with winter resting buds*

B — *In spring, the upper buds develop: the lower remain dormant*

C — *Removal of the upper part of the shoot causes lower buds to develop*

D — *Applying lanoline containing heteroauxin to cut end of shoot inhibits development of lateral buds*

thus accept the rather surprising fact that one and the same substance is capable of bringing about the elongation of newly formed cells and at the same time depressing the activity of cells in a state of division.[1]

Root growth

The relations between auxin and growth are less clear in roots than in stems. In spite of certain inconsistencies, the evidence on the whole indicates that removal of the root tip results in an increased rate of elongation, replacement of the tip bringing about a return to the normal rate of growth; in other words, a growth hormone is transported backwards from the root tip, but the effect produced on the region of extension is the opposite from that observed in the stem. There is no good reason for supposing that the growth hormones concerned are other than the same auxin-a and auxin-b produced by the stem tip, the difference being rather in the opposite nature of the reaction to these auxins on the part of stem and root.

This view is confirmed by the results of experiments in which heteroauxin is applied to roots. For example, when gelatine or lanolin containing heteroauxin is applied evenly over the cut surface of a decapitated root under suitable conditions for growth to take place, elongation ceases, contrasting with the increased elongation caused in a stem similarly treated; if

[1] There is experimental evidence that secondary meristems, such as the wood cambium, may be stimulated to increased activity of division in presence of auxin.

FIGURE 26 [see page 80

Illustrating suppression of development of lateral buds by auxin. *A*—Woody shoot in dormant condition. *B*—In spring, lower buds remain dormant, suppressed by the auxin derived from the more apical and actively developing buds. *C*—Development of basal buds on removal of the upper part of the shoot. *D*—pruned shoot to the end of which heteroauxin has been applied; the failure of lateral buds to develop indicates that it is the presence of auxin that is responsible for the basal buds remaining dormant in the intact shoot.

applied to one side only of the cut surface, elongation is more rapid on the side away from the point of application than on that towards it, so accounting for the opposite response of the root from that of the shoot to the stimulus of gravity. Again, whilst the development of lateral buds on a shoot is hindered by applying heteroauxin, the production of lateral roots is stimulated. It appears, therefore, that the same growth hormones are operative but that they induce opposite effects on root and stem. Since solutions of auxin and heteroauxin are poisonous to plant cells in any but very weak concentrations, it has been suggested that these opposite reactions may be due to greater sensitiveness on the part of roots, concentrations of auxin which cause elongation of tissues of the stem being strong enough to have a depressant action on those of the root. On this hypothesis, solutions of auxin should bring about elongation of the root as of the stem if sufficiently low concentrations are used; some workers claim to have obtained experimental evidence in support of this.

In view of the fact that many fungi produce heteroauxin and that a large number of fungal species grow in soil, one is led to speculate on the effects produced by liberation of heteroauxin by soil fungi on roots in the vicinity. There is, indeed, evidence that stimulation of root growth, particularly of the development of lateral roots, does occur in the presence of certain soil fungi.

Rooting of cuttings

Growth-promoting substances have found practical application in horticulture.[1] Treatment of cuttings with substances that stimulate root production, such as heteroauxin, often increases to a marked degree the propensity of cuttings to form lateral roots when planted (Pl. 5, facing p. 29). The extent to which rooting capacity is increased by such treatment varies greatly in different species and in relation with the previous history of the plants. This variation in behaviour is to be expected

[1] Tincker, M. A. H. *Jour. Roy. Hort. Soc.*, *61*, 510, 1936; *63*, 210, 1938; *64*, 554, 1939. (Record of experiments with root-forming substances used for the propagation of cuttings.)

because the formation of lateral roots is a complex process and a supply of auxin only one of the factors upon which this depends. For example, sugar or other carbohydrate is necessary for the growth of any plant organ; supplying auxin in the absence of sufficient carbohydrate to provide the materials for growth can have little effect in increasing production of lateral roots. Cuttings made from shoots containing abundant food reserves may be expected, therefore, to form roots more readily than those made from shoots in which the food reserves are scanty, and to give a greater response to treatment with heteroauxin. Doubtless failure of cuttings of some species to form roots even after treatment with heteroauxin may be sometimes ascribed to shortage of the food materials necessary for growth. The time of year at which the cuttings are taken and the previous treatment of the parent plant are important in this connection. Moreover, although a supply of auxin and adequate nutritive materials are important factors for root production they are not the only ones.

In devising a technique for using heteroauxin to stimulate root production in cuttings two facts must be borne in mind: one, that heteroauxin is poisonous in all but very dilute solutions; the other, that while it stimulates initiation of root development it checks root elongation. The root-forming substance can be applied in various ways, as a lanolin paste, mixed with some adhesive powder such as talc, or in the form of a solution. If a solution is used, the cuttings are placed for twenty-four to forty-eight hours in a solution of 1/10,000 to 1/50,000 concentration; these conditions should allow for absorption of sufficient heteroauxin or other substance used to stimulate root initiation at the cut end, but only trial will show the most effective dosage in any particular case. In general, the strongest solution that is non-toxic gives the most effective response. The cuttings are then removed from the solution and the lower ends inserted in damp sand where the absorbed heteroauxin is gradually lost to a point when the concentration permits the root initials that have been formed to grow out and elongate. When this technique is used, the heteroauxin is carried upwards with the transpiration stream in the dead conducting vessels whence it diffuses downwards and eventually reaches the living tissues that give

rise to the lateral roots. It is evident that although heteroauxin cannot pass upwards through living cells, a solution of it can be carried up the dead wood vessels in a purely mechanical way.

Formation of auxin

If a plant is grown continuously in the dark, production of auxin by the growing stem tips steadily falls; moreover, auxin production by the stem tips is depressed if all the leaves on the shoot are removed. To plant physiologists these facts have suggested that some substance, which they have called an 'auxin precursor', is formed in the leaves and other green tissues in the light, thence carried to the stem tips and other regions characterized by auxin production, and there converted into auxin (fig. 27, A). It cannot be the auxin itself that is formed in the leaves and transported to the growing regions since, as we have seen, auxin can move only in a downwards direction through the living tissues of the stem (p. 74).

If a seedling is used instead of a fully grown plant, auxin production by the stem tip suffers no diminution when germination takes place in the dark so long as the seed reserves are intact; removal of the reserve tissues from the seedling, endosperm or cotyledons as the case may be, results in a rapid fall in auxin output by the shoot apex. From this it is argued that a supply of the 'auxin precursor' is stored in the seed reserves together with carbohydrates and other nutrients and with them distributed to different parts of the seedling at germination (fig. 27, B). In regions such as growing points it is converted forthwith into auxin which is then transported through the plant in a downwards direction only. There is no evidence that auxin itself is stored with the food reserves of the seed, nor if it were would it be able to travel upwards in the stem to reach the apex.

Both auxin-a and auxin-b are acids; although the chemical constitution of the so-called auxin-precursor has not been as yet definitely established, there is reason to believe that it consists of organic salts—'esters' as the chemist calls them—of these acids. Such esters of auxin-a have been prepared and they could

fulfil the role of an auxin-precursor in so far as they exhibit no activity as growth hormones and can diffuse freely in any direction through the tissues. Furthermore, esters readily undergo decomposition with the liberation of the free acid again and there is nothing unreasonable in supposing such a change to occur in the auxin-ester when it reaches the growing tip, the active ester yielding the active acid.[1]

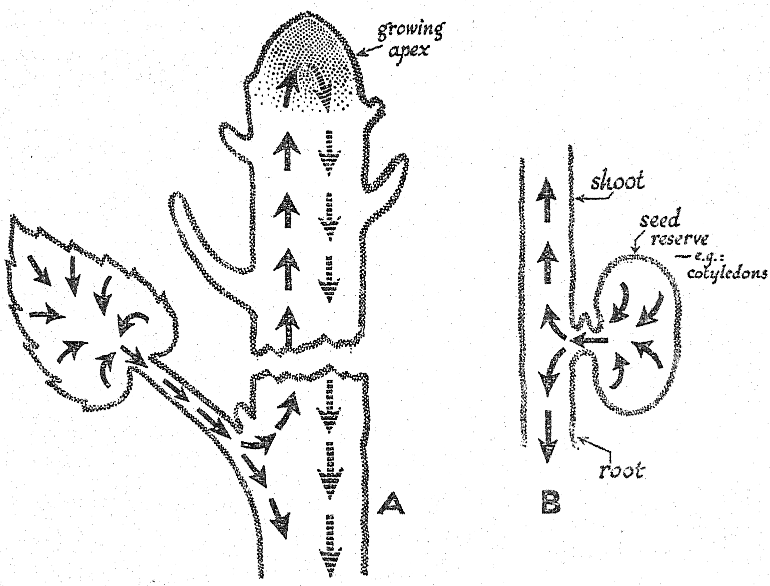


FIGURE 27

A—Diagram to illustrate the formation of auxin precursor in the leaves, its distribution in all directions in the stem, its conversion to auxin at the growing apex, and the transport of the auxin in a downwards direction only. *B*—Diagram to indicate how the auxin precursor stored in seed reserves is distributed throughout the seedling on germination.
Whole arrows represent movement of auxin precursor, broken arrows movement of auxin. C, seed reserve (e.g. cotyledons); s, shoot; r, root.

It follows from what has been said in the last few paragraphs that the development of roots by an isolated piece of stem is a

[1] That this kind of change does in fact occur is supported by the observation that the inactive ester tryptophane (indole–3–alamine) can be converted by fungi and bacteria into active heteroauxin (indole–3–acetic acid).

very much more complicated process than the gardener realizes when he hopefully 'takes cuttings'. If, as in ordinary garden practice, the cutting is dependent on auxin of its own production for stimulating root growth, it must be allowed to carry some buds or developing leaves since it is from these that the auxin is derived; it should also possess some fully developed leaves or other chlorophyll-containing tissue able to manufacture the auxin-precursor which on reaching the buds can be converted into auxin to replace that lost by diffusion downwards to the region of root production. Apart from this, the presence of leaves enables the cutting to manufacture sugar, important for root growth if food reserves in the stem are small in amount. On the other hand, the possession of leaves involves a continuous loss of water vapour and for this reason constitutes a risk that a stem may lose more water than can be afforded with safety until new roots are functioning. In practice, the successful gardener strikes a working compromise between removing all leaves so as to reduce loss of water as much as possible until new roots have been formed, and allowing all leaves to remain, so ensuring a maximum supply of auxin for the encouragement of rooting with a maximum food supply to provide the material and energy for the growth of new roots—not that he thinks in these terms, the technique adopted being based rather on his practical experience of the behaviour of different kinds of cuttings.

Incidentally, the common experience that keeping cuttings for any length of time standing in water—'to keep them fresh'—has an adverse effect on their rooting when subsequently planted can be explained as due to loss by diffusion of auxin which otherwise would accumulate in the base of the stem to a concentration favourable to root development. Loss in the same way of soluble food materials such as sugar doubtless tends also to lower the rooting capacity of the cutting.

Growth-controlling substances other than auxins

The fact that heteroauxin is a comparatively simple chemical substance that can be produced synthetically in any amount

required suggested to botanists exploration of the effects of other chemical substances on growth. As a result of such inquiry it has been found that a considerable number of other compounds produce comparable results when present as traces; they vary in efficiency being in general less effective than either of the auxins or than heteroauxin (indole-acetic acid) whether formed naturally or produced synthetically. Among them are many other indole compounds, e.g. indole butyric acid, as well as unrelated complex substances, α-naphthaline-acetic acid, phenyl-acrylic acid and many others. Many relatively simple compounds are also effective, of which ethylene (C_2H_4), acetylene (C_2H_2) and carbon monoxide (CO) may be cited as examples. As with the two auxins and heteroauxin, most are toxic in any but low concentrations. In high concentration some produce tumours and distortions of growth suggestive of virus diseases. Since the injurious effects vary greatly in different species, certain of these substances have been used with considerable success as 'selective' weed killers. Thus, a solution of fifty parts per million of α-naphthyl-acetic acid applied to the soil has no effect on the germination of Oat but reduces that of Charlock 82 per cent; solutions of even 300 p.p.m. do not affect the germination of Oat more than 2 per cent while completely suppressing Charlock. More remarkable still is the selective effect of 4-methyl-phenoxy-acetic acid which, broadly speaking, may be regarded as suppressing the growth of dicotyledons but not that of monocotyledons: at a concentration of 200 p.p.m. for instance, growth of Plantain (*Plantago major*) and Yarrow (*Achillea millefolium*) is completely inhibited and that of Corn Buttercup (*Ranunculus arvensis*), Fat Hen (*Chenopodium album*), Corn Marigold (*Chrysanthemum segetum*), Corn Spurrey (*Spergularia arvensis*) and Field Poppy (*Papaver rhoeas*) seriously affected, while that of Wheat, Barley, Rye, Oats, etc., is not impaired.[1] Another selective weedkiller with which extensive tests have been made recently is methyl-chloro-phenoxy-acetic acid to which the name 'Methoxone' has been applied. This also does not injure cereals

[1] Templeman, W. G. and Sexton, W. A. 'The differential effect of plant growth substances and other compounds upon plant species. I.' *Proc. Roy. Soc.*, *133*, 300, 1946.

and grasses at a dilution that kills or severely injures many common dicotyledonous weeds. It is said to be highly effective against Horsetail (*Equisetum* spp.) but to have little action on mosses in lawns.[1] There is an obvious opening for the employment of these compounds and others having similar properties for diminishing weeds from grass lawns[2] and for destroying dicotyledonous weeds from cereal crops.[3] It is perhaps too early to evaluate the usefulness of these newly available substances in agriculture and horticulture. The immediate effect of their application may be beneficial in so far as they eliminate unwanted weeds, but the balance between the soil micro-organisms may also be disturbed with a possible loss of soil fertility and the favouring of pathogenic soil micro-organisms. The toxic effects are claimed to be of relatively short duration, that of methoxone disappearing after four to five months.

A feature about some of these substances is that they may reach the tissues upon which they exert their effects in a more direct way than do the auxins. The latter, produced in the stem apex, and substances like heteroauxin, when applied in solution to the end of a decapitated stem, arrive at the regions that respond to their presence by comparatively slow one-directional transport in watery solution through living tissues, although no doubt if introduced into the dead conducting strands they can be carried upwards in the ascending water current. Gases such as ethylene, on the other hand, diffuse rapidly throughout the tissues and so exert their effects on all parts of the plant in a very short time. The effects of non-volatile water-soluble substances transported through the living tissues are thus more or less localized, whilst those of volatile substances that can diffuse through the air spaces within the plant are widespread.

Many of the chemical substances that give rise to effects resembling those due to the two auxins and heteroauxin probably never occur naturally in plant tissues; some, however, such as

[1] Tincker, M. A. H. 'Tests made at Wisley with a selective weed-killer methone.' *Jour. Roy. Hort. Soc.*, *71*, 141, 1946.

[2] Dawson, R. B. and Escritt, J. R. 'The use of growth-promoting substances for weed control in sports turf.' *Nature 158*, 748, 1946.

[3] Kraus, E. J. and Mitchell. 'Growth-regulating substances as herbicides.' *Bot. Gaz. 108*, 301, 1947.

ethylene, frequently do so. The production of ethylene is specially associated with the ripening stages of certain fruits, traces of this gas enormously accelerating the ripening processes (p. 100). Whether control of the latter kind comes within the definition of hormone action depends on whether the ethylene is produced by tissues other than those it affects, concerning which we have as yet no information. Acetylene and other substances that can exert control of growth processes, but are not produced by plant tissues, obviously fall outside the definition of a hormone as a 'chemical messenger' produced in one part of an organism but regulating activity elsewhere; they may be referred to as 'growth-controlling substances' but not as 'growth hormones'.

Some investigators regard auxin-a, auxin-b and heteroauxin as the only true growth hormones, and consider that the numerous other substances known to produce growth effects, do so not by direct action, but by modifying production or activity of the naturally occurring auxins; they claim, in short, that in the absence of a supply of auxin these other substances are without effect. However this may be, the point of practical interest is that, since these substances produce results in the plant that closely resemble those of the naturally occurring auxins, they may be employed in place of the latter for such purposes as the stimulation of root formation in cuttings. The practical man is not at all interested in knowing whether their action is direct or indirect; he is concerned to know whether the result he requires is encouraged by their use, also in the fact that many of them are far more readily available and less expensive than the natural auxins. That some of these substances are highly effective in promoting the formation of roots may be judged from the photographs shown in Pl. 5; facing p. 29.

Summary

It may be helpful to summarize the main facts that have been dealt with in this chapter in order to make clear their relations with one another.

1. A number of chemical substances when present in traces so small as to be hardly if at all recognizable by chemical means are able to modify the growth of the higher plants in various ways.

2. Outstanding among these are the auxins—auxin-a and auxin-b—of Flowering Plants. These originate in the apical parts of all organs that are actively elongating, such as terminal buds on growing stems, young leaves on growing petioles, flower buds on elongating flower stalks and the like. Indeed, the fact that a tissue is elongating may be taken as an indication that a centre of auxin production is situated somewhere above it.

3. The auxins are transported from growing regions where cell divisions are taking place to other parts of the plant through the living tissues in a downward direction only; as a result of this one-way transport they reach tissues below their point of origin where they bring about characteristic effects in certain regions, such as promotion of stem elongation, inhibition of the development of lateral buds, initiation of lateral roots and—when distributed unequally—the production of growth curvatures.

4. The reactions of roots to the auxins are in general the opposite to those shown by stems; elongation is reduced, activity of lateral roots is stimulated in contrast to the inhibition of lateral buds, and growth curvatures are towards the side of greatest concentration when the distribution of auxin is unequal, i.e. the reverse of the reaction that takes place in stems.

5. This system of control within Flowering Plants is analogous to the hormone systems regulating animal behaviour in that a substance produced in one part of the organism is transported to and exercises control upon development or behaviour in some distant region.

6. It would appear that the auxins are derived from an 'auxin precursor' which requires the presence of chlorophyll and light for its formation: the auxin-precursor may be either transported to the growing points and other regions of auxin production to be immediately converted into auxin, or it may be stored for future use in the same way as are reserve food substances. There are reasons for thinking that the auxin-precursor may be chemically an ester of auxin. Such esters have been prepared

and have been found to be inactive and not limited to one-way movement through living tissues; a simple chemical change (hydrolysis) at the growing point would set free the active auxin.

7. Among lower plants, especially fungi, a substance called heteroauxin is found. This is of simpler chemical composition than the two auxins, neither of which occurs in the lower plant groups, but is indistinguishable from them in its physiological reactions on the higher plants. Heteroauxin also occurs in some animal tissues and secretions; it can be made synthetically in the laboratory.

8. The facts that have accumulated about the two auxins provide a framework within which many of the commonly observed phenomena of plant growth in addition to simple stem elongation find a place. Other substances, either met with in nature or supplied artificially, may to a greater or less degree modify this main system of growth control. Such interesting facts as the enlargement of cells that frequently accompanies invasion of tissues by fungi or bacteria, or the stimulus to root formation in the early stages of germination that is associated in some plants with the presence of certain fungi, may or may not find an explanation in the excretion of heteroauxin or similar substance by the lower organism. The nature of such correlations invites fuller investigation.

9. Besides the two auxins and heteroauxin, a large number of other substances have been found to induce similar growth effects when present in traces: some of these, such as ethylene, may arise as normal products of vital activity; others, like acetylene, carbon monoxide, etc., are probably not encountered under normal conditions of life. How far these substances are to be regarded as acting directly on growth processes or as producing their effects by modifying the production or distribution of the auxins is at present a matter of controversy. Their interest from a practical point of view is that, whether directly or indirectly, they do produce comparable effects on growth under many conditions and are far more readily available in quantity than the auxins and heteroauxin produced naturally. Heteroauxin can be produced synthetically without difficulty and is used on a commercial scale as are other synthetic growth-con-

trolling substances, for regulating such growth activities as the formation of roots by cuttings. A recent application is the production of fruits from flowers when pollination has failed to occur or been ineffective (p. 170).

10. From the facts that have been discussed in this chapter it appears that a Flowering Plant exercises control on its development and on its growth reactions to external stimuli largely by the production and regulated distribution of auxins. Protean as are the effects of the auxins on growth and development, it can hardly be supposed that there are not other growth-controlling substances in plants, no doubt as important in their way but possibly more subtle and less obvious in their effects. Already there are more than hints that such exist, but at the moment the auxins and heteroauxin stand alone among naturally produced growth regulators in the completeness of our knowledge regarding their constitution and the manner in which they bring about control of plant activities.

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Chapter 4

SEASONAL CONTROL

We would be somewhat taken aback if in England we found snowdrops in full bloom in June or July or Michaelmas daisies flowering in February. The flowering of the former in spring and of the latter in autumn has come to be regarded as so much a matter of course that we tend to lose sight of the really remarkable feature about this behaviour; namely, that the flowering period of these plants should be so restricted, or, more generally, that in this climate the flowering of many plants is limited to certain definite seasons.

Inquiry into this behaviour has shown that the flowering of plants depends on the interaction of a number of different factors, some of them surprising and unexpected. Although it cannot be claimed that the mechanism controlling time of flowering is yet fully understood, enough has been learned about it to permit the botanist to alter experimentally the normal time of flowering of many plant species and induce them to flower at any time of year desired.

In order to appreciate the nature of this control it is necessary to understand something of what happens during flower development. Two main stages may be distinguished: the production of the flower rudiments, and the further development of these minute structures into mature flowers.

Following germination of the seed, a plant increases in size as a result of the activity of the growing regions at the ends of stems and roots; these regions of active growth may increase enormously in number as the plant becomes older and develops

lateral organs. At a particular stage of development, certain stem growing points pass from a vegetative to a reproductive condition, laying down rudiments of flowers instead of foliage leaves. Normally, all the dividing cells of the stem apex are used in constructing the flower, so that growth of the stem comes to an end with flower formation.

In perennial plants this change usually recurs annually at the same season, Dog's Mercury (*Mercurialis perennis*), for instance, flowering from March to May and Ivy (*Hedera Helix*) in October or November; more rarely a species may flower more than once each year, as occurs sometimes in the Globe Flower (*Trollius europaeus*) which may produce flowers in autumn as well as in May; sometimes flowering takes place after an interval of several years, as happens in certain Bamboos, e.g. *Bambusa arundinacea* which flowers every thirty-two years or so in India, and in Beech (*Fagus sylvatica*) and other trees which flower and fruit at intervals of a few years. Of annual and ephemeral species, some have a short and well-defined flowering season; such are Whitlow Grass (*Erophila verna*) which flowers from March to June varying with the district and season and Corn Cockle (*Lychnis Githago*) flowering in July and August; others like Shepherd's Purse (*Capsella Bursa-pastoris*) and Chickweed (*Stellaria media*) may be found in bloom from February to November or even during the winter in mild weather, several generations following one another in the course of the year.

One aspect of our problem, therefore, is to determine the causes for this change-over from vegetative to reproductive activity; another is to discover what conditions permit or encourage the development of these rudimentary flower buds into fully formed flowers, conditions that may or may not be the same as those favouring the development of vegetative buds. It is convenient to consider first this second stage of flower development.

Dormancy: relation with low temperature

Of the conditions that limit the development of any growing plant organ, one of the most important is temperature. Within

certain limits, the rate of growth usually declines as the temperature falls, eventually ceasing altogether. We can readily understand, therefore, why the flowers of Aconites, Snowdrops, Willows and other spring-flowering species, rudiments of which were laid down during the previous autumn, do not develop until the cold of winter is over; the same considerations apply also to resting vegetative buds formed at the end of the summer.

The minimum temperature at which growth of flower buds can go on varies greatly for different species and for some is surprisingly low. As an example of the latter may be cited the little Soldanellas ('Glory of the Snow') of the Swiss Alps, the flowers of which may be found opening before the snow covering has completely disappeared from the ground in spring. At these high altitudes, the sun's rays, penetrating the thin layer of snow, warm the underlying soil sufficiently to start the flower buds into growth; even so, the temperature at which these flowers unfold cannot be far above freezing point and must fall below this at night.

In all cases in which flower rudiments or vegetative buds are formed late in the year and growth of all kinds brought to an end by the cold of winter, it might be expected that a rise of temperature would be sufficient to induce the flowers or leaves to unfold. This is true, however, only within certain limits.

In this country, branches of Willow (*Salix* spp.), *Forsythia*, and other spring-flowering trees and shrubs, cut in early February and brought into a warm room or greenhouse, open their flower buds and unfold their leaves while branches on plants outside exposed to prevailing low temperatures are inhibited from doing so. It is evident that the growth of both flower and vegetative buds is held back in February solely by low temperature. If, however, the experiment is carried out on the same species of plant in late November, although the buds differ in appearance little if at all from their condition in February, no further development takes place in spite of the favourable temperature. How can this dramatic contrast in behaviour be explained?

Further light on the conditions that determine the opening of resting buds may be obtained by bringing branches into a warm

greenhouse and standing them in water at intervals from November onwards. Only after a certain critical date has been passed will the buds on such branches respond to the higher temperature to which they are exposed. This date is not the same every year, but follows a period of cold weather; in short, the buds require to be 'wintered' before a rise of temperature will induce growth. Without such exposure to cold, the buds remain more or less permanently dormant however favourable the temperature for growth, so that a spring-flowering plant kept in a warm greenhouse during the whole of the winter does not, as might be expected, come into flower and leaf earlier than one left outside, but may, on the contrary, retain its dormant condition far into the summer, producing flowers and leaves irregularly and often months later than plants of the same species out of doors that have received a 'cold stimulus' and so been rendered capable of responding to the warmth of spring (fig. 28).

There are thus two stages in the winter dormancy of such plants: one depending on internal causes or physiological factors, the restraining effects of which on growth can be removed by exposure to a low temperature for a short time; the other imposed directly by the external low temperature. Raising the temperature does not remove internal dormancy and is effective in stimulating growth activity only when the internal factors have ceased to operate.

This behaviour of flower and leaf buds in a state of winter rest extends to many seeds and spores. If the ripe seeds of Beech, Ash and many other trees and shrubs are dried, they acquire dormancy as a result of which germination will not take place or will be irregular or delayed when they are placed under suitable conditions for germination in spring, unless they have been previously allowed to absorb water and been exposed to a low temperature. Perfectly dry seeds, it should be noted, do not lose dormancy as a result of exposure to low temperature. For this reason, seeds collected in the autumn and required for sowing the following spring should not be stored dry indoors at room temperature, but kept in damp sand out of doors during the winter; under this treatment they are automatically exposed to periods of low temperature while in a moist condition

and will be capable of unrestricted germination subsequently. This treatment of seeds is known technically as *stratification*; some seeds require to be 'stratified' to ensure full and even germination, others do not.

A point of minor interest is that the different growing regions

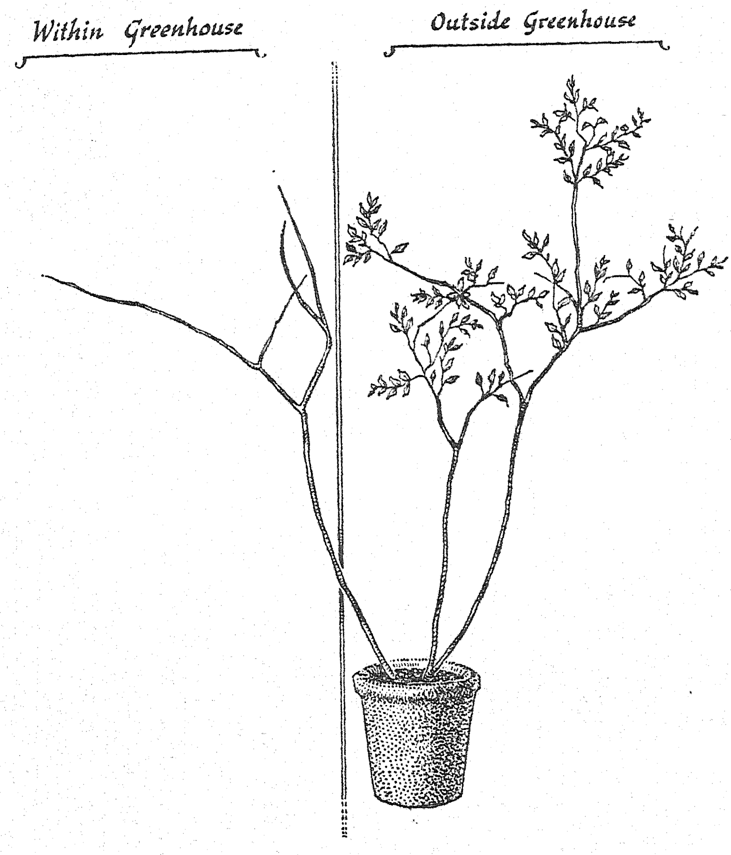

FIGURE 28

The effect of cold in breaking the dormancy of resting winter buds. On Feb. 21st a pot plant of *Vaccinium corymbosum* was placed outside a greenhouse, but the single branch on the left was passed through the glass into the warm interior. The drawing shows the condition of the plant on May 21st. The branch that had not been exposed to periods of cold out of doors had remained dormant, that exposed to a cold stimulus had come into leaf.

of a plant that have become dormant in autumn may not all require the same degree of cold stimulus to allow growth to start when the temperature is subsequently raised. If bulbs of Hyacinth are exposed to warmth after an insufficiently long period of exposure to a low temperature, the leaves will grow and elongate but the flower scape, requiring longer exposure to cold for complete removal of its internal dormancy than do the leaves, may remain short and stunted. Examples of this behaviour are sometimes provided by the amateur gardener when, becoming impatient for his bulbs to come into bloom, he begins to force them in a warm room or greenhouse before they have been exposed for a sufficiently long period to lower temperatures.

Buds, seeds, and other resting structures must have reached a certain stage of development before exposure to a low temperature has any effect in removing internal dormancy. Under natural conditions a cold period may come early or late in the winter according to the season, but is not likely to come until considerably after the time when it could first exert its influence. When eventually the cold period has been experienced and the internal dormancy removed, growth may be still delayed since in all probability it will be some time before conditions are sufficiently warm for growth, i.e. before the external cause of dormancy is removed.

An obvious way to bring spring flowers into bloom earlier than happens naturally is to curtail the delay that occurs at the two critical stages: first to provide artificially a cold period as soon as the dormant structures have reached a stage of development at which low temperature is effective; then to expose them immediately to the warmth of a room or greenhouse, instead of awaiting the uncertain onset of the natural warmth of spring. The degree of earliness that can be achieved by these means varies with the kind of plant, depending on how soon the buds reach a stage when exposure to cold becomes effective in removing inherent dormancy; also on the length of time that a low temperature must be maintained before the buds can be stimulated by subsequent exposure to warmer conditions. These considerations apply both to flower buds and vegetative

buds and also to seeds, when dormancy of the latter is due to internal or physiological causes and not to peculiarities in the structure of the seed-coat that inhibit germination.

Retarded flowering

Temperature control may be used to induce flowering out of season in another way. Blooms can be obtained *earlier* than in nature by artificially shortening the period of internal and external dormancy; obviously they may also be obtained *later* by prolonging artificially the low temperature conditions of winter. Although spring flowers that are a month or so overdue are of no interest to the florist, it may be a very different matter commercially if such delay can be extended to nine or ten months, since flowers can be put on the market a couple of months or so before they are expected and thus a ready sale ensured. The fact that they are not really next spring's flowers before their time, but those of last spring long-delayed is not realized by the ordinary purchaser.

Among the plants that can be 'retarded' in this way successfully on a commercial scale and appear on the market as 'early spring flowers' is Lily-of-the-Valley (*Convallaria majalis*) which naturally flowers in May or June. The commercial grower is here faced with an interesting psychological problem: How far in advance of the expected flowering season will a flower most attract public taste? A flower appearing naturally in June will fetch a higher price in April than in May, in February it is likely to be in even greater demand, but the market value will not continue to rise indefinitely in correspondence with the number of weeks before its natural flowering time; in November, for instance, the demand for it would probably be much less. In addition to an enhanced out-of-season value, account must be taken of the scarcity of flowers of all kinds during the winter months and of the special demands at the Christmas season.

Dormancy: removal by factors other than low temperature

Treatments other than exposure to cold have been found to be

effective in overcoming internal dormancy and have been exploited on a commercial scale; among such are exposure to high temperatures or to the vapour of anaesthetics, and the use of various chemical substances. It has been suggested that a common feature of the effects produced by all these treatments is an alteration in the permeability of the living protoplasm of such a kind that substances can migrate more readily from one part to another within a cell, and also pass more readily through the thin skin or pellicle of living protoplasm that separates one cell from another, so facilitating chemical reactions involved in the change from dormancy to active growth. The agent used in any particular case depends on the responsiveness of the plant species concerned and on practical convenience.

Anaesthetics such as ether or chloroform are frequently used to overcome the internal dormancy of Lilac (*Syringa vulgaris*) and of other flowering shrubs that form their flowerbuds in the autumn; by raising the temperature these are then forced into bloom for the Christmas market or earlier. Cut branches are put in a gas-tight chamber together with sufficient ether to form a low percentage of vapour (e.g. 0·5 per cent), the amount of ether used and the time it is allowed to act varying with the kind of plant. After this treatment the branches are removed and forced into bloom in a warm greenhouse.

For bulbs, such as those of Tulip, Daffodil and the like, preliminary exposure to a high temperature is the treatment usually employed. The procedure consists in steeping the bulbs for some hours in hot water—at a temperature of about 170° F. —before forcing. This treatment serves the double purpose of overcoming the internal dormancy and of killing the external growth of moulds and other fungi apt to be present on the bulb scales.

Gaseous substances other than ether or chloroform that have been found effective for hastening the life-cycle are ethylene (a component of coal gas), acetylene, carbon monoxide and others.

One of the most important practical applications of ethylene is concerned not with its effect on flower buds, but with the marked acceleration produced in the ripening of many fruits. Oranges or lemons picked unripe for transport often arrive at

their destination still green; if they are given a short exposure to traces of ethylene they quickly assume the orange or yellow colour of the mature fruit and become more readily saleable. This effect of ethylene of hastening the ripening processes of fruits may, on occasion, be embarrassing, since in some cases the fruit, as it approaches ripeness (but not while unripe) itself evolves appreciable amounts of ethylene. Under natural conditions this rapidly diffuses away and is probably of little importance, but it is otherwise when such fruits are packed together in large numbers in a closed space as in the hold of a ship; the inclusion of ripe fruit may cause the percentage of ethylene to become sufficiently high to bring about rapid ripening of the whole cargo before its arrival in port. For these reasons, in loading bananas great care is taken to avoid inclusion of a bunch on which any fruit is sufficiently advanced in ripeness to give off ethyelene; inclusion of a single ripe bunch may involve the loss of a large part or even the whole of the cargo owing to premature ripening.

As an instance of the commercial use of acetylene for stimulating growth may be mentioned its employment as a cheap and satisfactory method for 'breaking' the dormancy of young potato tubers. Young newly formed tubers are sometimes required for planting as 'seed', but the difficulty is encountered that such tubers are very slow to start growth. If, however, they are steeped in water to which a little calcium carbide has been added (at the rate of eight ounces to eleven gallons of water) for four or five hours before planting this difficulty disappears.[1] Those who have used acetylene lamps will remember that acetylene is liberated when calcium carbide is moistened.

Vernalization

We now pass to the second aspect of our problem as stated at the beginning of this chapter (p. 94). So far we have considered ways by which control of the development of rudiments

[1] Hutton, E. M. 'Breaking dormancy of the potato.' *Jour. Council for Scientific and Industrial Research, Canberra, Australia, 15*, 262, 1942.

already laid down in the flower bud can be exercised; we have seen that similar methods are applicable to dormant vegetative buds, resting seeds, tubers—in fact to all growing plant organs that show periodic stages of dormancy in the course of their development due to other than structural features. The causes that determine the laying down of flower rudiments in place of those of vegetative organs are still far from understood except in a quite superficial way; it is known that certain cultural treatments favour the former, but exactly how and why they do so is still in part a matter for speculation.

Here again it appears that temperature is one of the important factors concerned. A remarkable example of the way in which flower organization depends upon the previous history of the plant in respect to temperature experiences, and one that has important practical bearings, is provided by the series of phenomena known collectively under the term *vernalization.* Vernalization concerns the effects that follow special temperature treatment of the seed before sowing, and may be well illustrated in reference to wheat.

There are two classes of wheat in cultivation, described as spring and winter wheats respectively. Spring wheats are varieties which flower later in the same year if sown in spring; winter wheats are sown in autumn, pass through the winter as small seedlings and flower the following summer. If a winter variety of wheat is sown in the spring it forms flowering spikes or 'heads' too late in the season to ripen or may not even flower at all.

It was discovered as far back as the middle of the last century that winter wheat could be made to behave like spring wheat in respect to flowering by subjecting the seed to appropriate treatment before sowing, such treatment replacing the 'wintering' to which winter wheat is naturally exposed when sown in the autumn. At the time, the discovery of this fact was regarded as of no more than academic interest, and it is only within the last twenty years that it has been applied for the benefit of agriculture. The process, known as vernalization, to which winter wheat is subjected in order to bring about flowering in the same year it is sown, is simple enough. The seed is moistened in order to

provoke the onset of germination; either it is soaked in water for about twenty-four hours but not long enough for germination activities to become fully established, or alternatively, given only half the amount of water needed for complete swelling and germination. It is then subjected to a temperature near freezing point for several days. The seed may then be sown immediately, when it will behave like spring wheat, flowering and fruiting the same summer; or it may be dried and stored to be sown later if the weather at the time is still unsuitable for spring sowing (Pl. 6; facing p. 128). The substitution of an artificial cold period for the natural cold of winter is not effective if the seed is dry but only if water has been absorbed and the conditions for initiation of germination provided. Incidentally, it is of interest to note that this process is reversible; if winter wheat that has been vernalized is subjected to a high temperature, it behaves once more as a normal winter variety.[1]

In this country and in the grain-growing areas of North America, vernalization would appear to have little practical importance. Winter wheats have certain advantages in regard to yield and quality of flour over spring wheats, and in our climate the severity of the winter does not preclude the cultivation of winter wheats whenever the farm routine permits of its being planted. In parts of Russia, however, there are two climatic reasons that contribute to make vernalization of great value: early onset of severity of winter conditions may make autumn sowing impracticable, while severe drought in late summer may require early ripening. This explains why much of the work concerning the application of vernalization to large-scale growing of cereal crops has come from the Soviet Union.

The vernalization process is best known with respect to its application to wheat and other cereals, but it has been claimed that a great variety of other crops benefit from similar treatment in regard to the resultant acceleration of flowering under the climatic conditions that exist in many parts of the Soviet Union.

The behaviour of vernalized wheat recalls in some ways the

[1] Purvis, O. N. and Gregory, F. G. 'Devernalization by high temperature.' *Nature 155*, 113, 1945.

effects of cold in removing the internal dormancy of resting winter flower buds, so hastening the formation of mature flowers; but there is the important difference that in the former the effect is not upon the development of structures already present but upon that of others not yet in existence; the vernalization process pre-determines the behaviour of the growing point in respect to its future—often far distant—conversion from a leaf bud into a flower bud. Perhaps the two most remarkable features about this process are: first, that there is no intimation that any change has been produced until many months after treatment, and secondly, the fact that after germination has presumably started the seed can be returned to a resting condition without loss of vitality, rendering dry storage possible until it is required for sowing.

Recent researches have shown that the whole phenomenon of vernalization is more complex than at one time thought; that the response to vernalization treatment may be largely influenced by factors other than the temperature of the environment.

Photoperiodism

A quite different factor that has been found to control the time of production of flower buds and hence of flowering is, rather unexpectedly, 'length-of-day', a phenomenon known to plant physiologists under the somewhat ponderous term of *photoperiodism*. By 'length-of-day' is meant the number of hours out of the twenty-four during which the growing plant is exposed to light.

If different plant species are cultivated under conditions so controlled artificially that one series is given six hours' light every day, another series nine hours' light, a third series twelve hours' and yet another series sixteen hours', they fall into three groups in respect to their flowering behaviour.[1]

One group consists of species that come into flower under short-day illumination but remain in the vegetative condition when the period of daily illumination is long. Examples of such

[1] Garner, W. W. and Allard, H. A. *Jour. Agric. Res.*, *18*, 553, 1920.

short-day plants are the Scarlet Runner Bean (*Phaseolus multiflorus*) of our vegetable gardens, *Cosmos grandiflora*, many varieties of Chrysanthemum, Michaelmas Daisies, Asters, and other plants of the flower border. A second group, exemplified by Sweet Vernal Grass (*Anthoxanthum odoratum*) and Jerusalem Artichoke (*Helianthus tuberosus*), contains species that bloom only when given a long period of illumination each day; under short-day illumination flowering is delayed or postponed indefinitely. A third group contains species like the Annual Meadow Grass (*Poa annua*) that flower indifferently under short-day or long-day illumination—the so-called 'ever-blooming' types. This diverse behaviour depends solely on the period of illumination given each day and is quite independent of the intensity of the light (Pl. 7; facing p. 129).

Further consideration of the species constituting each group reveals the fact that those in the first group, flowering only under short-day illumination, are all plants that flower naturally in spring or autumn; those of the second group, the long-day species, those that flower naturally in summer; while in the third group are those that may be found in flower at any season. These observations suggest that the reason why certain species flower in spring or autumn is that at this time of year the days are short, and that others flower in summer because they are long-day plants requiring the long days of summer for the production of flower buds; species that flower at any time of year must be insensitive to the effects of length-of-day on the production of flower buds. In the light of these considerations it is perhaps not surprising that some spring-flowering plants, such as the Globe Flower (*Trollius* sp.), bloom a second time in autumn, a season when once more the days are short.

Knowledge that the formation of flower buds depends on length-of-day provides a means of controlling the time of year at which a plant flowers, or of checking flowering at the normal time. If late-flowering varieties of Chrysanthemum, for example, are given long-day illumination from midsummer onwards by artificial means, they fail to flower; it is as though they were waiting for the short days of autumn—which never arrive! On the other hand, if the plants are allowed to receive only nine

hours of light a day from late spring onwards, they will come into flower many weeks before their normal flowering time when the days have become naturally short.

Control of length-of-day is practicable only on an experimental scale; it has little application in large scale flower production for market. In the domain of plant breeding, however, it may have considerable commercial importance. For example, no opportunity is presented for hybridization or inter-crossing of many plants that flower naturally at different seasons of the year. By artificially altering the length-of-day for one or both species, the times of flowering can be made to overlap and cross-pollination rendered possible.

Exactly why the formation of flower buds is correlated with length-of-day or why a long day provides the requisite conditions for some plants and a short day for others provides problems that still puzzle the botanist. No doubt this behaviour is bound up with attainment of a particular balance between the products of the chemical activities within the plant. Such horticultural practices as pruning, ringing, root pruning of fruit trees, designed to encourage the production of flower buds, probably operate in a similar way by modifying the extent of those chemical reactions that depend on exposure of a leaf surface to light and by interfering with the transport within the plant of water and the nutrients dissolved in it. In this connection what is referred to as the carbon-nitrogen ratio has been specially stressed, by which is meant broadly the relative proportions of carbohydrates and nitrogen-containing compounds the plant is able to manufacture under the conditions in which it is grown, a low proportion of the latter class of compound appearing to favour flower production.

Reviewing all these observations, it is evident that the time of flowering of plants is controlled by a number of different factors that may be interrelated in complicated ways, and that the season when any plant species flowers depends on its particular reaction to these different factors. Picturing the case of a short-day plant that is able to grow at a comparatively low temperature level, growth may be expected to start early in spring when the short days at this time of year will induce it to

form flower buds; it will be a spring-flowering species. On the other hand, a short-day plant requiring a higher temperature level for growth will start activity later, so much later perhaps that the days have already lengthened before it has had time to form flower buds. Having missed this early opportunity, it will have to await the return of short days in autumn before it can produce flower buds; it will consequently be an autumn-flowering species. In some cases we may imagine that the rate of response to short-day illumination is so sluggish that rudiments of flower buds are not laid down until quite late in the autumn, so late that their further development is postponed by the onset of winter until the return of warm weather with the following spring; plants that behave in this way would constitute the species that flower in early spring from buds laid down the previous autumn as in so many of our fruit trees.

This imaginary picture of the factors at work in the case of short-day plants is no doubt unduly simplified. It assumes, for instance, that the failure of flower buds organized late in autumn to unfold the same year is due solely to the temperature being too low for growth, whereas we have seen that such buds do not develop even when the temperature is artificially raised, but may require to be subjected to a still lower temperature, such as may be expected in winter, to remove the 'internal' dormancy (p. 96).

It has been suggested by Lysenko, the Russian botanist, that in the life cycle of many plants there are definite phases which are passed through in a fixed order, completion of one phase being necessary before the next can begin. On this view, there is a phase of vegetative growth, vigorous or sluggish, long sustained or brief; only when this phase is completed can the *quality* of growth change and another, the reproductive phase, begin. Completion of the former phase is largely dependent on appropriate temperature sequences, control of the latter frequently on length-of-day. There is general agreement among botanists that a distinction should be made between growth and development—between mere increase in size and the change from one stage in the life history to another: there is, however, considerable disagreement with Lysenko's view that these stages must

be of necessity passed through in a fixed order and are irreversible. Recent work has shown that the reactions of plants to their surroundings are far more complex than was realized when Lysenko's views were first propounded, the reaction to any one factor being greatly influenced by other factors in operation or that have operated in the past.[1] Apart from such complexities, however, these investigations have revealed a number of methods by means of which the time of flowering can be controlled, many of which are of practical importance to horticulturists and growers.

Summary

The foregoing pages have shown that the production of flowers by a plant, accepted so much as a matter of course that most people give little thought to the underlying causes, is in fact a highly complex business, requiring among other things a correct sequence of low and high temperatures together with a 'length-of-day' that is characteristic for the particular species under observation. In view of all the conditions and limitations known to govern flower production one is almost surprised that plants ever succeed in flowering at all! It should not occasion surprise that plant species often behave very differently in respect to flowering when removed from their natural habitat to another dissimilar environment; rather is one amazed at the powers of adjustment that enable them in so many cases to continue to produce flowers under conditions in which the factors controlling flower production are so widely different from those to which they have been accustomed. On the practical side, a study of the nature of many of these factors has indicated various ways by which the time and abundance of flowering may be controlled artificially. Modification of the natural flowering season may be of importance to the flower trade; to agriculture if it allows a crop to ripen which, if it flowered at the natural time, would be injured by the climate of the locality; and to the plant breeder in that it enables him to hybridize varieties or species that bloom naturally at different seasons.

[1] Whyte, R. O. 'Phasic development of plants.' *Biolog. Revs 14*, 51, 1939.

To end this chapter, the different ways in which time of flowering can be controlled artificially are briefly summarized

A. Treatments that lead to the production of flower rudiments in place of leaf buds

1. Vernalization: the provision artificially of a short low-temperature period during incipient germination. This accelerates production of flower rudiments in many plant species the seedlings of which normally undergo, but have not received, a cold period.

2. Photoperiodism: artificial control of the number of hours of light to which a plant is exposed, usually described as 'length-of-day'.[1] This probably operates by altering the chemical balance within the plant, so causing production or suppression of flower rudiments in many species.

3. Application of horticultural operations such as pruning, ringing, root pruning, etc. These, no doubt for similar reasons to those mentioned under 2, modify the degree to which vegetative activity is replaced by reproductive organization.

B. Treatments that affect the development of flower rudiments already present

1. Exposure to artificially produced low or high temperatures, or to various chemical substances such as ether, chloroform, ethylene, etc., may remove the 'internal' dormancy of buds that under natural conditions must await a period of severe cold weather.

2. Exposure to a warm temperature (50°–80° F.) or 'forcing', *after* the internal dormancy has been removed, accelerates the development of resting buds still held in check out of doors by a naturally occurring low temperature. Forcing is ineffective *before* the internal dormancy has been removed.

3. Exposure to continuous low temperature, below that required for growth, delays the development of resting buds beyond the period naturally imposed by the climate. Species

[1] There seems reason to believe that it is the period of continuous darkness rather than the period of illumination that is the determining factor.

differ in respect to how long development can be delayed in this way without injury; in some the delay may be extended to several months, in which case the so-called 'retarded' flowers may simulate precocious blooming.

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Chapter 5

PLANT NUTRIENTS

Whilst the manner and degree of growth and development in plants may be controlled by chemical substances like auxins or by environmental conditions such as temperature, period of illumination and so on, a fundamental condition for the occurrence of growth of any kind is a supply of nutritive materials from which may be obtained the chemical elements necessary for building new tissues. A general idea of the elements present in these constructive materials can be acquired from chemical analyses of plant tissues. These tell us that some few elements are always present in considerable amounts, whilst many more are present in much smaller quantities. (Table I, p. 112.) It may be presumed that the former are necessary constituents of a plant's food, but experimental investigation is required before it can be decided which of the latter are essential and which occur merely because they happen to be present in the surroundings and enter the plant in the absence of any mechanism to exclude them. That some of the elements found are not really essential to the well-being of the plant concerned is suggested by the fact that their presence is not invariable.

Plant nutrition—essential elements

Quite early in the study of plant nutrition the method of investigation by growing plants in water culture was brought into use. The experimental plants are grown with their roots in

solutions of known chemical constitution prepared from mineral salts; variation of the culture fluid by additions or omissions of certain of the nutrient salts provides a means for estimating the effects produced by particular salts on growth and development. A modification of this method, known as sand culture, is often substituted. The experimental plants are grown in quartz sand, ground pumice or other insoluble granular material, thoroughly washed to remove all nutrients, and then flooded with a culture solution containing known mineral salts. These culture methods, originally devised for testing the nutritive value of different solutions in the laboratory, have been recently exploited for growing plants on a commercial scale (p. 127). Obviously, both water and sand cultures can be used to test the nutritive value of substances other than mineral salts.

Soon it was found that many plants could be grown satisfactorily for long periods if supplied with various mixtures of mineral salts in watery solution, but that in order to obtain complete and healthy growth certain chemical elements must be *always* represented in the mixture. Such were designated 'essential elements'; they are comparatively few in number and were, by this experimental method, found to be: hydrogen, oxygen, nitrogen, phosphorus, sulphur, calcium, magnesium, potassium and iron. Examples of complete culture solutions are given in Table II.

A wide variety of such solutions have been used by different workers; so long as all the essential elements are represented and the total concentration is not allowed to become too high normal growth may be expected, although the formula that gives optimal growth varies with the species of plant. The dependence of plants on a supply of, say, potassium or sulphur can be demonstrated by replacing the potassium salts or sulphates by corresponding sodium salts or chlorides in one of these culture solutions; appropriate substitutions suffice to show the indispensability of other elements to a plant's normal growth. If an essential element is omitted from the culture fluid, growth and health are adversely affected and certain *deficiency* symptoms are exhibited the precision of which depend on the species of plant under observation and on the particular

TABLE I

Percentage weight of the elements composing a mature Maize plant obtained from an analysis on five plants. (Data from Miller—*Plant Physiology*, 1938.)

	Percentage of the total dry weight
Oxygen	44·431
Carbon	43·569
Hydrogen	6·244
Nitrogen	1·459
Phosphorus	0·203
Potassium	0·921
Calcium	0·227
Magnesium	0·179
Sulphur	0·167
Iron	0·083
Silicon	1·172
Aluminium	0·107
Chlorine	0·143
Manganese	0·035
Undetermined elements	0·933

TABLE II

Examples of complete culture solutions.

Sachs' solution 1860		*Knop's solution 1865*		*Shive's solution 1915*	
KNO_3	1·00 gms.	$Ca(NO_3)_2$	0·8 gms.	KH_2PO_4	2·450 gms.
$Ca_3(PO_4)_2$	0·50 ,,	KNO_3	0·2 ,,	$Ca(NO_3)_2$	1·228 ,,
$MgSO_4$	0·50 ,,	KH_2PO_4	0·2 ,,	$MgSO_4$	3·697 ,,
$CaSO_4$	0·50 ,,	$MgSO_4$	0·2 ,,	$FePO_4$	0·004 ,,
$NaCl$	0·25 ,,	$FePO_4$	trace	H_2O	1,000 c.c.
$FeSO_4$	trace	H_2O	1,000 c.c.		
H_2O	1,000 c.c.				

element omitted. A knowledge of the characteristic symptoms that develop in the absence of any element from a culture solution enables deficiency of this element in a soil to be deduced from the behaviour of plants growing in it. (The development of deficiency symptoms from the absence of elements other than those mentioned above will be discussed later, p. 118.) Some plants are more sensitive to lack of a particular element than are others; those that are specially sensitive and develop well-defined symptoms to shortage may be conveniently used as 'indicator plants' for determining whether or not the element in question is available in the rooting medium. In forming an opinion as to whether or not infertility is due to some mineral deficiency, deductions from the behaviour of growing plants are often more informative than the results of chemical analyses; the latter may show indeed whether an element, as a constituent of some compound, is present or not, but the former will indicate whether it can be utilized by a growing plant in the form in which it occurs—which is what the cultivator requires to know.

The method of water culture served to show that, broadly speaking, ordinary green Flowering Plants growing in light can obtain all they require for growth and well-being if their roots are supplied with a dilute solution of mineral salts in which the nine essential elements mentioned are represented.

It may be noticed that carbon does not appear in the list of essential elements as determined from water culture experiments although it forms a notable proportion of plant tissues. This is because, unlike other constructional elements, carbon is not derived from the solution in contact with the roots but from the carbon dioxide of the air. The utilization of this source of carbon for the building up of complex carbon compounds such as sugars, cellulose, proteins, etc., requires energy to be supplied; in green plants this energy is derived from that part of sunlight that is absorbed by the green pigment chlorophyll. This process of synthesis induced by light energy, known as *photosynthesis*, occurs therefore only in the green parts of plants when these are exposed to light in presence of carbon dioxide. The energy absorbed from the light in the construction of these organic compounds is set free again on their disintegration and

becomes available for the various life processes requiring energy for their accomplishment. This yielding up of the potential energy resident in organic compounds by living organisms is known broadly as *respiration*; in plants it consists typically in the oxidation of sugars, although many other chemical reactions resulting in the liberation of energy may be concerned.

Although the extent to which any particular element is absorbed may be modified by the concentration of other constituents of the solution, the proportions in which these elements are represented is, within limits, not of critical importance. This is because the plant is able in great measure to select the materials it requires irrespective of their relative abundance in the culture solution; that is to say, there is no direct relation between the proportions in which the elements occur in the solution (or in the soil) and those in which they are absorbed by the plant. How widely different may be the proportion in which an element is present in the tissues of a plant and in the nutrient supply to which it has access is exemplified by the Brown Seaweeds which absorb and accumulate iodine in such large amounts that they constitute a commercial source of iodine, although iodine can be detected with difficulty by chemical means as a constituent of the sea water from which the plants obtain it. Again, although Ling (*Calluna vulgaris*) is confined to acid soils in which the calcium content is low, the tissues are crowded with crystals of calcium oxalate. On the other hand, aluminium compounds enter largely into the constitution of clay soils, yet aluminium occurs in insignificant amounts in most plant tissues.

Loss and replacement of nutrients

The mineral nutrients in an artificial culture solution become depleted through absorption by roots; the soluble nutrients are removed from soil in a similar way, but here there may be in addition considerable losses in the drainage water. The extent to which losses of the latter kind occur is governed by two factors: solubility of the substance concerned and retentiveness of

the soil towards it. A substance such as calcium sulphate is very insoluble and its removal in the drainage water inevitably slow; nitrates are highly soluble and so disappear rapidly. The second factor is a result of retention of substances in the soil solution by chemical and electrical attractive forces present at the surfaces of soil particles. This kind of retention, known as *adsorption*, is a surface effect and therefore shown in greatest degree by the clay and organic constituents of soil, because the very numerous small particles of which these are composed represent a relatively large total surface compared with that possessed by a corresponding volume of larger particles. The degree of retention also varies with the nature of the substance in solution. Thus, the rapid removal of nitrates or salts of magnesium from soil in the drainage water depends not only on their ready solubility but also on the fact that their surface retention is slight; phosphates, on the other hand, are removed from a soil by leaching with difficulty because, apart from any considerations as to their solubility, they are strongly adsorbed on the surface of the soil particles. The degree of retentiveness of a soil for any substance may change in accordance with the treatment the soil may have received. In view of these facts it is not surprising that the amount of nitrates in natural soils is often less than is required by plants for maximum growth, thus leading to severe competition for any nitrates present, or that the magnesium content of many soils is low and not infrequently reaches deficiency levels.

Under natural conditions the loss of nutrients from a soil as the result of absorption by plants is not a permanent loss, since the elements taken from the soil and built up into plant tissues are returned to the soil again during the processes of decay following the death of the plant. (See Chapter 6.) In nature, therefore, the fertility of a soil, in so far as this depends on its content of mineral food, is not rapidly or permanently impaired as a result of plants growing in it. Under the cultural conditions of agriculture or horticulture, however, much of the plant material forming the crop is removed and the soil becomes impoverished in elements which under natural conditions would have been eventually returned to it. Consequently it becomes necessary to replace these in some way if the soil is not to become

progressively less fertile as successive crops are taken from it. This replacement can be carried out broadly speaking in two ways, either by adding organic matter such as plant or animal refuse, or by adding inorganic chemical compounds or 'artificial' fertilizers.

The former corresponds closely to the natural way in which the fertility of the soil is restored and is the traditional method; its effectiveness has been proved over centuries of use. It has the drawback that organic debris is bulky to handle and involves higher labour costs both in collection and application than does the application of mineral fertilizers.

The latter practice is relatively modern, dating from about the middle of the nineteenth century by which time it had been established that green plants obtain their carbon from the carbon dioxide of the air and the other elements they require by absorbing mineral salts from the soil. In gaining acceptance for this view the influence of Liebig was outstanding; many of his conclusions were incorrect but the main outline of his theory stands and the stimulus he gave to soil investigation can be hardly over-estimated. Artificial fertilizers are mainly derived as by-products from gas works, smelting works, chemical factories and the like, although some are obtained from natural deposits all of which are probably of organic origin; their large-scale use may be regarded as an outcome of the enormous quantities of such by-products at the disposal of industry following the industrial revolution. Compared with organic manures, artificial fertilizers have the advantage of greater ease and less cost of application and the theoretical appearance of greater economy in that it is necessary to apply only compounds containing those elements of which the plant has run short.

We are not concerned to discuss here the claims that have been put forward for and against these two systems—the so-called 'compost controversy'. The subject is complex and controversial, but there is fairly general agreement on one point; namely, that the continued use of inorganic fertilizers *only* tends to lower seriously the humus content of the soil and to destroy its physical structure. Other consequences that follow failure to supply sufficient organic material to soils that are continuously

cropped or that suffer from too generous an application of 'artificials' are considered in the next chapter.

Minor or trace elements

The results obtained from early experiments in which plants were grown in water or sand cultures supplied with a solution of known composition, together with those that followed additions of mineral salts to crops, appeared to establish the basic nature of a green plant's requirements in the way of soil nutrients. These were concluded to be an adequate supply of mineral salts in which the essential elements nitrogen, phosphorus, sulphur, potassium, calcium, magnesium and iron were all represented.

Although practical experience in general confirmed this point of view, yet certain areas were known in which a particular crop could not be raised successfully although routine soil analyses showed none of the expected deficiencies usually associated with infertile soils; moreover, there was the further peculiarity that while swedes might consistently fail, barley would yield a satisfactory crop. The explanation of such anomalous behaviour was eventually provided by the discovery that plants require for satisfactory growth small traces of a number of elements in addition to those already recognized as 'essential', and that the soils in question were deficient in one or more of these. This discovery was made possible only by the availability of salts of a far higher degree of purity for making up culture solutions than had been accessible to the earlier experimenters.

The first of these 'trace elements' to be clearly recognized was boron,[1] although considerable evidence had been brought forward in respect to manganese five years previously (1922).[2] It had long been known that plants of Broad Bean were difficult to grow to the final stages of development in the usual water culture solution although the reason for the difficulty was

[1] Brenchley, W. E. and Warrington, K. 'The role of boron in the growth of plants.' *Ann. Bot.*, *41*, 167, 1927.

[2] McHaigue, J. S. 'The role of manganese in plants.' *Jour. Am. Chem. Soc.*, *44*, 1592, 1922.

obscure. The symptoms observed were that before the flowering stage was reached the growing points became disorganized and blackened and soon the plants died.

It so happened that in some experiments carried out in 1927 at Rothamsted, designed to determine if the addition of mild poisons to a culture solution in which Broad Beans were growing would check attack by Black Aphis, boracic acid was one of the substances tested. The unforeseen result of the experiment was that, although the boracic acid had no effect in discouraging the aphids, the bean plants in the cultures receiving it developed to maturity, forming flowers and fruits. Further investigation showed that to enable beans to complete their life cycle a supply of boron is necessary although the amount required is remarkably small, being a few parts per million. The dependence on such small traces of a substance can be recognized with certainty only if highly purified salts are used in making up the culture solutions, otherwise the trace element may be included unwittingly among the impurities. For example, the need for supplying boron in the culture solution may be unrecognized if plants are grown in vessels of glass into the manufacture of which boron enters, sufficient boron being dissolved from the glass to satisfy the plant's small requirements.

Some plants are much more sensitive than others to the absence of boron; leguminous plants such as beans are highly sensitive, thus accounting for these plants being the first in which a need for boron for complete growth was recognized. Small as is the boron requirement of beans, grasses and cereals need even less, although all species appear to require some boron for normal growth. The smaller the boron requirement the less is a plant species likely to suffer from deficiency of this element in nature.

In addition to boron, the elements of manganese, zinc and copper[1] among others have been shown to be essential in small amounts for all species of plants hitherto tested; molybdenum is known to be essential for certain fungi and bacteria and is

[1] Bailey, L. F. and McHaigue, J. S. 'Copper deficiency in tomatoes.' *Am. Jour. Bot.*, *30*, 358, 1943.

probably required by other plants as well, e.g. Cauliflowers;[1] there are indications that silicon and aluminium should be added to a list likely to be still further extended by future researches. That the symptoms shown by a plant are due to deficiency of some minor element may be confirmed by the recovery of normal growth when a compound containing the element in question is added to the soil: it is more satisfactory, however, to inject the compound into the plant tissues since failure to obtain a response in the former case may be due to a reaction with the soil that renders the compound unavailable to plant roots.[2] Experiments to demonstrate the essential nature of an element required only in minute traces need meticulous care in order to exclude any accidental source of the element under investigation, such as absorption from the containers of the culture solution or introduction in the form of dust particles.

The fact that these trace elements are required in such small amounts suggests that they are not used as constituents of plant tissues, but rather that they serve to facilitate in some way the chemical changes involved in growth. Substances that facilitate chemical change without themselves forming part of the final product are known in chemistry as *catalysts.* One function of trace elements may well be to catalyse some of the chemical reactions necessary for growth.

Summarizing present views regarding mineral nutrients: certain elements known as 'essential elements' must be represented in the mineral salts available for absorption by the roots of green plants if normal growth and complete development is to occur. These fall into one of two categories: the 'major' essential elements that are required in quantity since they form the materials of which the plant body is built up, and the 'minor' or 'trace' elements required in minute amounts only since they serve by their presence to facilitate chemical reactions associated with growth processes without themselves permanently enter-

[1] Davies, E. B. 'A case of molybdenum deficiency in New Zealand'. *Nature*, *156*, 391, 1945.

[2] Lal, B. N. 'Plant-injection methods for the diagnosis of mineral deficiencies in Tobacco and Soya Bean'. *Ann. Bot.* (N.S.) *9*, 283, 1945.

ing into the compounds formed and as a consequence being used up.

In view of the relatively small amounts of iron required compared with those of the other major essential elements, it is probable that iron should be included rightly with the trace elements; that considerably higher concentrations are called for in the case of iron than of other trace elements may be due to the readiness with which iron forms in the soil compounds inaccessible to plant roots.

The position of magnesium is also somewhat anomalous. It is a 'structural' element in that it is a component of chlorophyll, although quite small amounts in the soil suffice for the needs of most plants; on the other hand, magnesium is also essential for the growth of non-green plants such as fungi, where it must play some role other than that of contributing to the construction of chlorophyll.

Since trace elements are required in such small amounts, it seems improbable that any of them will be deficient or likely to become so in natural soils, or even in agricultural soils that are continuously cropped, as may be the case with nitrogen, potassium, and other elements that are used in large quantities for the construction of plant tissues. Nevertheless, areas are known in various parts of the world in which one or more of the trace elements is below the level required by some plants. Soils in which the manganese content is too low for crops like swedes that have a relatively high manganese requirement, although high enough for barley with a low manganese requirement, are not uncommon. As with major essential elements, deficiency of a minor essential element in a soil can be conveniently recognized by the reactions of 'indicator' plants—plants that have a high requirement for the element in question and at the same time develop characteristic symptoms when there is insufficient of it for their needs. Such indicator plants are specially valuable in the case of trace elements since failure to detect such elements by standard methods of chemical analysis is no proof that the minute amounts required by plants may not be present.

As an example of a disease due to manganese deficiency may be cited that known as 'grey speck' affecting oats which may

cause complete failure of the crop. Symptoms indicating a deficiency in this element are specially liable to develop on soils rich in organic matter and lime; they are almost unknown on acid soils.

Recent work on the absorption of manganese by roots from soil emphasizes the need to distinguish between an absolute lack of an element and its presence in a form unavailable to the roots.[1 2] Moreover many soils diagnosed as deficient in manganese by the symptoms developed by crops grown on them and by the virtual absence of manganese in the crop itself, often have been found to contain considerable quantities of manganese when subjected to chemical analysis. This anomaly is due to manganese existing in the soil in several forms, only one of which is available to plant roots. Since 'manganese deficient' soils may contain abundant manganese dioxide, it appears that in this fully oxidized tetravalent form manganese is not available. Many bacteria in the presence of certain organic substances can reduce manganese dioxide to divalent forms such as manganese sulphate, the action being accelerated in the presence of glucose and other carbohydrates that provide food for the bacteria. The converse change—oxidation of manganese sulphate to the unavailable manganese dioxide—occurs partly as a direct chemical action and partly under the influence of micro-organisms. How much of the manganese in the soil is available depends therefore on the relative rate at which oxidative and reduction processes are occurring, which in turn depends largely on which set of organisms is most favoured by the conditions in the soil at the moment. The development of 'manganese deficiency' in a soil is thus not a simple matter of presence or absence of manganese, but depends on moisture, aeration, temperature, acidity, and all the other factors that control the activities of micro-organisms.

Correction of a deficiency in a trace element is usually brought about easily and cheaply in the field; owing to the very small quantities required, broadcasting a few pounds or less per acre

[1] J. H. Quastel. 'Soil metabolism.' Roy. Inst. of Chem. Lecture, 27th April 1945. Pub. 1946.

[2] Mann and Quastel, *Nature*, *158*, 154, 1946.

of some compound containing the element or elements in short supply suffices as a rule to remove the deficiency symptoms for a long period of time.

In making widespread application of a compound of a trace element it must be remembered that only minute traces of the element are required and that the presence in the soil of larger quantities may be harmful to plant growth.

Before closing this section it should be pointed out perhaps that *trace elements*, required by plants only in very small amounts, are not to be confused with *tracer elements*, used to follow the behaviour of an element when it enters the living system of a plant or animal. All atoms of an element have similar chemical properties, but they have not necessarily the same mass. Atoms of an element having a mass differing from the normal are known as *isotopes*, and although they are chemically indistinguishable from normal atoms they can be recognized by physical means. Thus, if the food of a plant or animal contains a phosphorus compound in which the phosphorus atoms are some isotope of phosphorus instead of ordinary phosphorus, exactly what happens to this phosphorus in the body of the plant or animal can be determined because it can be distinguished from the phosphorus already present by physical means although it will behave normally in all its chemical reactions. This is becoming an important new method of research in physiology owing to recently devised methods of producing isotopes of different elements that can be used as tracer elements. It has already been shown, for example, that phosphorus taken into the body in a meal will have found its way into the bones within a very few hours.

Deficiency diseases

The practical importance of minor or trace elements has been increasingly recognized in recent years. In many soils the amounts of them available may not be so low as to cause deficiency symptoms even in plants having relatively high requirements, yet the addition of compounds containing them

often results in improved crop growth. Indeed, the application of trace elements in the small quantities that satisfy plant needs is so simple and inexpensive that there is much to be said for the treatment of any soils at all under suspicion with a mixture of manganese and boron compounds—the trace elements most frequently deficient—before waiting for deficiency symptoms to develop. At the same time it must be borne in mind that in excess—sometimes in very small excess—of the small amounts required, compounds containing these elements may prove toxic; there are plant disorders attributable to excess as well as to deficiency of trace elements.

Another aspect of this matter concerns the dependence of animals, including man, on trace elements. Certain disorders in grazing stock have been shown to be due to a deficiency of some minor element in the soil and hence in the herbage; in some cases, as with copper and manganese, these elements are essential also to plant growth, in others, as with iodine and cobalt, they do not appear to be essential plant nutrients. Thus goitre and thyroid gland diseases of sheep as well as in man have been associated with a lack of iodine in their feed. A deficiency of copper is held to be responsible for various diseases of sheep and cattle in different parts of the world, an example being the disease known as 'swayback' affecting lambs. Copper appears also to be essential for haemoglobin formation, so that a form of anaemia may develop in its absence although abundant iron is available. Besides promoting the conversion of absorbed iron into haemoglobin, copper is essential also in many oxidation changes, a number of oxidizing enzymes having been shown to be copper-protein compounds. In parts of Australia and New Zealand a type of wasting disease in cattle has been traced to a deficiency of cobalt in soil and herbage. Chickens have been shown to be sensitive to manganese deficiency in their food; and so on.

Mineral toxicity

In contrast to animal diseases due to some mineral deficiency in their food plants, disorders may be caused by the presence of

a poisonous mineral substance in some component of the herbage. Poisonous elements are rarely absorbed from the soil by food plants in sufficient quantity to render them dangerous to animals. As a rule, any plants that do absorb poisonous mineral compounds that happen to be present in the soil will be themselves killed and the surviving vegetation will consist of those species that can almost completely exclude the poisonous substances from their tissues. Exceptions occur, however, in the cases of compounds of fluorine and selenium.

Normally, compounds of fluorine occur so sparsely in soils that there is no need to take them into account. But whilst in this country soils containing sufficient fluorine to produce toxicity in the vegetation are rare, in some parts of the world, the State of New Mexico for example, they are sufficiently common and the effects sufficiently serious for survey maps to have been prepared in which are indicated the areas in which the fluorine content is dangerously high. Cattle grazing in these areas develop characteristic disorders leading among other symptoms to a brown mottling of the teeth, and their eventual loss. Human beings are similarly affected by the use of locally grown vegetables or of the local water for drinking or cooking. Fortunately the fluorine can be removed from the water by simple treatment.

The metal selenium has already been mentioned in reference to 'indicator plants' (p. 18): it has also considerable interest in the present connection. In certain arid and semi-arid regions of the United States of America and elsewhere there occurs among animals a form of sickness, often proving fatal, to which local names—'alkali disease', 'blind staggers', 'loco disease'—have been given. All these regions contain appreciable amounts of selenium in the soil and the disease has been proved to be directly associated with the presence of selenium in the herbage.[1] [2] [3]

[1] Trelease, S. F. and Martin, A. L. 'Plants made poisonous by selenium absorbed from the soil.' *Bot. Rev. 2*, 373, 1936.

[2] Trelease, S. F. and Trelease, H. M. 'Selenium as a stimulating and possibly essential element for indicator plants.' *Am. Jour. Bot., 25*, 372, 1938.

[3] Beath, O. A. 'Toxic vegetation growing on the Salt Wash Sandstone member of the Morrison Formation.' *Am. Jour. Bot., 30*, 698, 1943.

Investigation has revealed the fact that comparatively few plant species can absorb selenium from the soil in an inorganic form; a few, however, can do so. For some of these selenium appears to be an essential trace element (p. 118) and they are confined to seleniferous soils for which they serve as indicators; for others there is no evidence that the selenium absorbed is essential to them. Among them are species of the leguminous genus *Astragalus*, notably *A. bisulcatus*, normally fodder plants; such plants are usually present in large quantities in areas where the disease is prevalent and are undoubtedly mainly responsible for it. On the other hand, crops such as maize, oats or wheat can be raised on these seleniferous soils and fed without ill effects to cattle or man, because these cereals do not absorb the inorganic selenium compounds present. If, however, the land carries a growth of seleniferous plants such as *Astragalus bisulcatus* and this is ploughed in before sowing the cereals, the subsequent cereal crop will be strongly toxic to animals eating it. Thus, it appears that plants such as cereals while unable to absorb selenium from the soil in an inorganic form can do so as organic selenium compounds in the humus derived from the decay of seleniferous plants. For this reason *Astragalus bisulcatus* and other species behaving in the same way have been called 'selenium converters'; in their absence crops can be grown safely on soils containing selenium. As might be expected, where highly seleniferous plants occur in dense patches, the grasses growing near them become toxic owing to the dead foliage of the former decomposing in the soil, so providing the grasses with organic selenium compounds that can be absorbed by their roots.

This behaviour of plants towards the absorption of selenium is of considerable interest in connection with a matter discussed earlier in this chapter; namely, the relative advantages of supplying plants with the essential elements they need in the form of mineral salts or of humus (p. 117). The fact that most plants find a difficulty in absorbing inorganic selenium compounds but no difficulty when the selenium forms part of the humus complex, suggests that the same may be true for other elements—that in general plants may be able to obtain some of the elements they need more readily from the breakdown products of humus

than from inorganic salts. No doubt one of the reasons for most plants failing to absorb inorganic selenium compounds from soils is that these are for the most part highly insoluble, extremely stable and resistant to root action by most plants, but the same is also true if in rather less degree of essential elements such as phosphorus which may well be more easily available for absorption by roots when presented in organic form as existing in humus or other organic debris than when given as inorganic phosphates.

Hydroponics

Increased knowledge of the mineral requirements of plants has naturally led to greatly increased success in growing plants in water culture, so it is not surprising that attempts have been made to cultivate plants in this way on a commercial scale. Of the methods employed the one that has proved most generally successful is a modification of the laboratory sand culture in which the roots of the plants are grown in some inert solid medium, such as ground pumice or sand, irrigated with the culture fluid. Perhaps the best known form of this type of culture is that known as *hydroponics*; here, the solid medium in which the plants are growing is flooded at intervals with the culture fluid which is then allowed to drain back into a storage tank, ready to be used again for the next period of flooding. Machinery has been devised to carry out this periodic flooding and drainage automatically at determined intervals.

This method has the advantage of economy in use of the chemicals contained in the culture medium; moreover, during the drainage of the surplus liquid after flooding, air is drawn into the interstices of the sand, thus ensuring perfect aeration, while the roots are free to absorb the nutrients they require from the films of liquid adhering to the sand particles. The liquid in the storage tank is tested at intervals to determine what additional salts must be added in order to replace those removed by the plant roots.

The following are among the advantages claimed for such methods of culture. Complete control of the food materials sup-

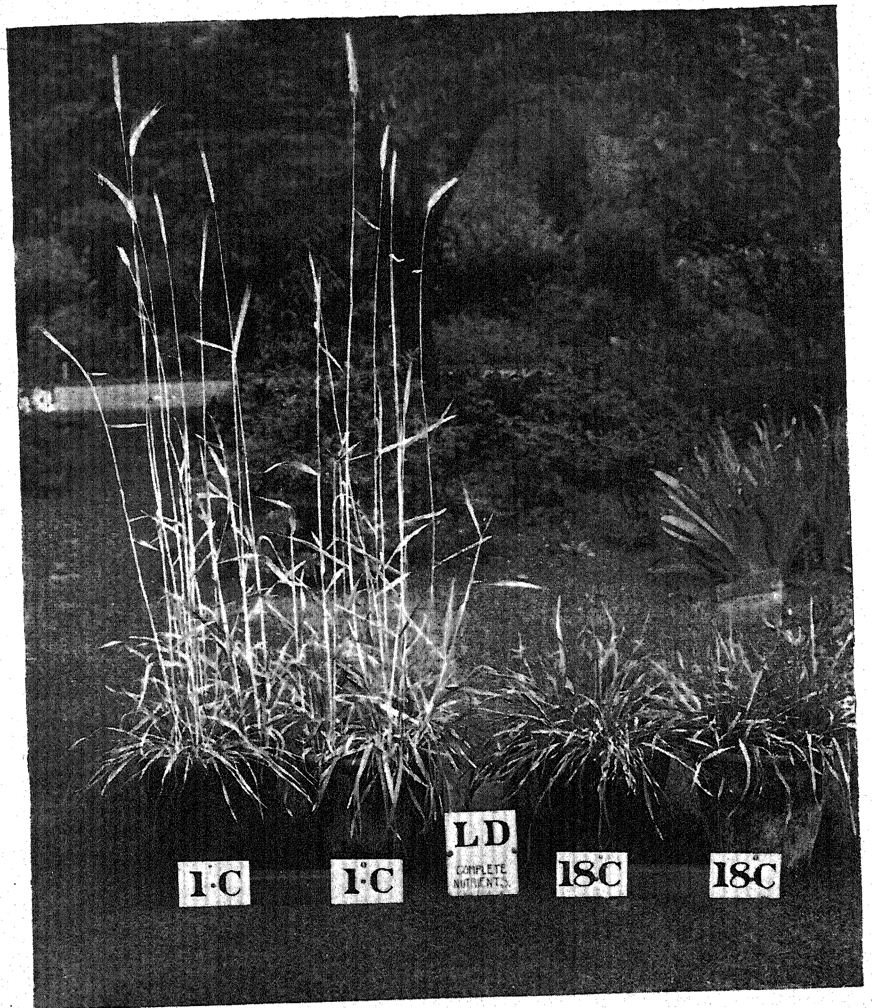
plied to the plant, the nature of which can be varied to accord with that desirable at each stage of development. Owing to the ease with which the rooting medium and culture solution can be sterilized, root diseases due to parasites can be largely eliminated, as can the competition for light and nutrients by weeds that accompany cultivation in natural unsterilized soil. Moreover, the crop is said to mature earlier and to yield a greater return per square yard of bed than when similar plants are grown in soil.

While it may be true, as its advocates point out, that cultural systems of this kind should provide opportunities for improved growth by reason of the precise control exercised over the environment at all stages, it seems unlikely that greatly increased yields can be expected. Apart from special circumstances, a fertile soil provides so adequately the mineral nutrients required by plants that no conditions however perfect are likely to raise the yield by more than a small percentage, an expectation borne out in practice. In general, probably the chief advantage of the method is the control that can be exercised on the incidence of root diseases.

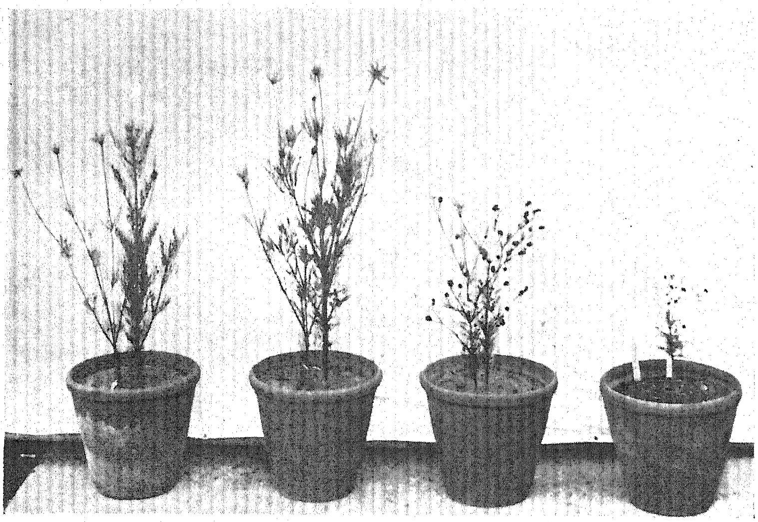
An important consideration in the case of edible crops is the extent to which the nutritive value may be affected. Chemical evidence provides no proof of loss in this respect, but comparison of the products of hydroponic culture with those obtained from soil culture by means of carefully controlled feeding experiments is required before the claim that the former are of equal nutritive value can be regarded as fully established.

Without question it has been demonstrated that, with the exercise of the necessary care and skill, certain plants, notably Carnations, Tomatoes, Lettuces and species of *Gerbera* can be grown with marked success by hydroponics; to which plant species this method can be extended with equal success remains to be proved, but results so far obtained suggest that the range may be limited. For reasons to be discussed in the next chapter it would not be unexpected if many kinds of plants failed to respond as favourably as when grown in soil.

It should be borne in mind that hydroponic culture, in spite of its apparent simplicity, calls for considerably more skill and



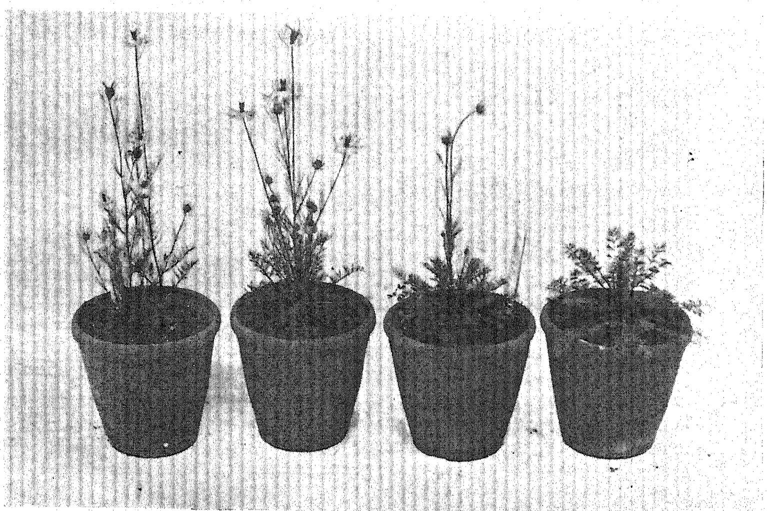
6. Vernalization—the effect of temperature on germination. The plants shown are Winter Rye, variety 'Petkus'. The seed was sown on the same day in all four cases, but the two pots on the left were kept at 1 °C. during germination, the two on the right at 18° C.; subsequent growth was at the same temperature for all. The letters LD indicate that all the plants received long-day illumination so that failure of the plants on the right to flower is not due to a light effect. Winter varieties of Wheat behave similarly; when sown in spring they only flower the same season if the seed is subjected to a low temperature during the early stages of germination.



(i) (ii) (iii) (iv)

7A. Photoperiodism; short-day plant

Cosmos bipinnatus: (i) control, i.e. natural length of day, plants with few flowers; (ii) seventeen hours' light per day—twelve hours' daylight and five hours' electric light: plants with few flowers; (iii) twelve hours' daylight only: plants with many flowers and ripening fruits; (iv) six hours' daylight only: plants with flowers and ripening fruits. Treatment from April 4th.



(i) (ii) (iii) (iv)

7B. Photoperiodism; long-day plant

Nigella damascena: (i) control: in flower; (ii) seventeen hours' light per day: in flower; (iii) twelve hours' daylight: in bud; (iv) six hours' daylight: vegetative growth only. Treatment from April 24th.

more constant attention from the cultivator than does soil culture. The growing plants must be kept under continuous observation and adjustments made in nutrients supplied in response to the reactions shown by the plants. The culture solution requires to be frequently checked to ensure that a suitable concentration and balance of salts is maintained and that it does not become too acid or too alkaline as ingredients are removed by the plant roots. The whole system is far more sensitive than when plants are grown in soil owing to the adsorptive powers of the latter. The humus fraction of soil in particular, owing to the extensive surface it possesses, is able to collect and hold soluble substances when present in excess in the soil water, and to liberate them again if the soil becomes deficient in any of them. In this way the soil behaves as a buffer, smoothing out and softening the results of excess or deficiency.

On the economic side, hydroponics and similar systems can have little application in this country outside greenhouse culture; it is only by comparison with other cultural methods under glass that it should be judged as a commercial proposition.

Although hydroponics has no place in general agriculture, it may prove valuable in large-scale cultivation under special climatic conditions, when, for example, there are long periods without rain and the water supply becomes the limiting factor for plant growth. An example of the value of hydroponics in special circumstances was provided by the use made of it in Ascension Island during the war.[1] The island was occupied by American troops; it is completely waterless, all water having to be brought in by ship. One of the problems for the army was provision of a constant supply of fresh vegetables and salads. A large hydroponic plant was constructed consisting of a series of concrete basins on the hillside filled with the local pumice ash. Culture fluid was fed into those at the top and by suitably arranged conduits found its way into the basins below. On reaching the lowest basin the solution was pumped up again to the top basin. Using this method, the troops stationed on the island were able to provide themselves with a constant supply of fresh lettuces

[1] *The National Geographic Magazine* (U.S.A.), *88*, 219, August 1945.

with the expenditure of a minimal quantity of water, losses from evaporation being reduced by a series of sun screens.

It is possible that similar methods may be found advantageous in arid conditions elsewhere in which water shortage and the porous nature of the ground make cultivation by ordinary irrigation methods impracticable.

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Chapter 6

PLANT GROWTH IN SOIL

In the last chapter we have considered some of the problems concerned with the culture of plants in an artificially simplified 'soil' consisting of particles of some insoluble material flooded with a weak solution of nutritive inorganic salts. In a natural soil the mineral particles are soluble in varying degree and there is also present *humus*, an important constituent, derived from the remains of plants and animals in various stages of decay.

Humus is not a single chemical substance, but a most complex mixture of organic materials ranging from undecomposed plant or animal tissues and secretions to the relatively simple final products of decay. Its chemical nature is complicated because the course followed during decay depends on the nature of the substances broken down, on the conditions under which decomposition occurs, and on the organisms responsible for the breakdown. Nevertheless, all kinds of humus give to the soil certain characteristics among which the following are conspicuous.

1. Good aeration owing to the cellular structure of plant tissues: addition of humus improves the aeration of soils in which it is deficient.

2. Owing to the extensive surface possessed by the materials composing humus, soils containing it have a large capacity for holding water and of retaining with great tenacity salts removed from the solution surrounding the soil particles. The latter process is known as adsorption (p. 116).

3. Many humus constituents can be used directly by lowly

organisms such as fungi and bacteria for which they provide an essential form of food. Consequently, well-aerated soils containing humus possess a profuse population of micro-organisms, both plant and animal.

4. The presence of these micro-organisms leads to profound secondary effects, not only from the nature of the by-products liberated during their activities, but also because they themselves are a source of food for other organisms and so form the starting point in the building up of a closely interlocked soil community.

5. Finally, humus is a reservoir of all the elements required for plant nutrition; although these are not for the most part present in a form directly available for absorption by the roots of vascular plants.

It is evident, therefore, that addition of humus, besides altering such physical characteristics as aeration and water-holding capacity, converts a dead medium composed of a collection of mineral particles into a soil teeming with life. The problems associated with the rooting medium in the absence of humus are mainly static, those in its presence dynamic. In the former case the factors involved are the relative abundance of particles of different size affecting porosity, the capacity for holding salts, and so on. Any of these can be evaluated as an isolated problem and the combined results used to describe the soil. In the latter case, in addition to the above factors there exist those depending on the presence of soil organisms. The kinds of organisms present and the activities in which each is engaged will be constantly altering as changes occur in the environment, changes that the activities of the organisms themselves help to bring about.

It is obvious, therefore, that the conditions controlling the nutrition of a vascular plant growing in soil are not simply those of a plant growing in sand culture to which another component, humus, possessing particular physical and chemical characteristics, has been added; with the introduction of humus a new series of complicated factors make their appearance owing to the biological activities of the micro-organisms that the humus contains and supports. It is with the various biological consequences

associated with the presence of humus in natural soils that the present chapter is mainly concerned. Those aspects of nutrition hitherto considered have been based on the assumption that there is a simple and more or less direct relation between nutrients supplied and their absorption by root hairs.

Nutrition with and without humus

The ordinary green Flowering Plant obtains the carbon it requires for building up its tissues from the carbon dioxide of the air; the methods of water culture described in the last chapter serve to demonstrate that all the other food elements needed can be obtained from a solution of appropriate mineral salts in contact with the roots.

Under natural conditions, such a solution exists as a continuous thin film around the soil particles. The mineral salts dissolved in it are continuously removed in the drainage water and by the absorptive action of roots, losses made good from two main sources, the inorganic rock particles which form the larger part of most soils and the humus. The former are not usually highly soluble, since the more easily dissolved constituents are early removed by the water percolating through the soil, leaving only the less soluble, which may, however, undergo more rapid solution under the action of secretions from plant roots. The latter—the humus—is not immediately available for absorption by roots, but under the disintegrating action of micro-organisms eventually yields up the mineral nutrients previously removed from the soil by the plants whose dead remains compose it. In other words, while the removal of soluble substances in the drainage water is to be regarded as a permanent loss from the soil, the elements removed in the form of mineral salts by roots are not lost permanently but on the death of the plant are returned to it again in the form of humus which thus constitutes an enormous potential reservoir of mineral nutrients. The conversion of these potential nutrients into forms that can be absorbed by roots is a much more complex process than mere solution, demanding, as it does, the co-operation of various

kinds of micro-organisms under the action of which the complex organic materials that form the starting point of humus are gradually broken down into substances of simpler chemical composition. The incorporation of dead plant tissues with the soil and the subsequent disintegrating activities of micro-organisms constitute highly important processes in maintaining the fertility of most soils; it calls not only for the presence of the requisite organisms, but equally for soil conditions favourable for their activities.

We have here one of the outstanding differences between artificial systems of culture such as hydroponics and the natural growth of plants in soil. In the former, the only mineral nutrients available are those supplied artificially in the form of inorganic salts, which become immediately available to the roots after undergoing a simple process of solution; in the latter, besides the inorganic particles of the soil an additional, indeed the most important, reserve of mineral nutrients is the humus. Maintenance of fertility of a natural soil is largely bound up with its content of humus and with the biological processes responsible for setting free its mineral nutrients. Soilless culture or hydroponics might indeed be described as plant culture without humus, since a collection of varying sized particles derived from disintegrated rock cannot properly be regarded as soil. Such a collection of particles, it is true, constitutes the first stage towards the formation of a soil and provides the framework of a mature soil, but until a humus (i.e. organic) component has been acquired the mixture cannot be regarded as 'soil'. One of the aims in soilless culture is to keep the rooting medium as free as possible from contamination by micro-organisms, whilst in a soil absence of the normal vast and varied micro-population or the disturbance of its activities leads often to cessation of humus breakdown, to the accumulation of peat and to infertility.

It is evident that the root environment and nutritive conditions of plants growing in natural soil with its essential content of humus are far more complex than those of a plant growing in any form of water or sand culture. In the former, the process of nutrition cannot be fully represented as simple absorption by the root of mineral salts dissolved in the soil

water. Account must be taken of the nutrients rendered available by the breakdown of humus by micro-organisms, and allowance must be made for the effect of beneficial or deleterious by-products and excretions that arise during the life activities of the innumerable kinds and numbers of organisms whose existence is rendered possible by the presence of humus. Apart from such complex interrelations, the soil micro-organisms react on higher plants and on one another through direct competition for any food materials they may have in common, or by direct parasitism on one another. So vast and complicated are the biological problems that arise from the presence of humus in the soil that no more than a general survey to indicate their extent and importance can be attempted.

As already noted, humus is not a chemical entity, but a convenient term for the mixture consisting of dead plant and animal remains together with the series of organic substances that result from their gradual decay. Chemically its constitution may be extremely varied, for the plant and animal remains will differ in chemical content with the kinds of plants and animals from which they have been derived. Furthermore, each chemical substance in these residues forms the starting point for a series of chemical changes in which the original substance is split by a succession of different micro-organisms, step by step, into simpler substances; the nature of the chemical compounds formed at each stage of breakdown depends on the organisms present, and the nature of these organisms as well as that of the products resulting from their activity vary with such environmental factors as temperature, aeration, acidity, and the presence of specific chemical substances, including those produced by the organisms themselves. In short, the character of the humus depends upon the kinds of initial substances present and the conditions under which the successive stages of their decomposition take place, both of which determine the kinds of organisms present and the nature of the products resulting from their activities. Any evaluation of the results of soil treatments, whether by physical cultivation or by the addition of chemical substances, must include not only their effects directly on vascular plants and on the physical and chemical characters of the

soil, but also those produced on the soil micro-flora and micro-fauna, modification of whose numbers and activities may in the long run lead indirectly to profound changes in the soil outweighing in importance those produced directly.

Biological cycles

Let us turn now to a more detailed consideration of some of these activities on the part of soil organisms.

In the first place there are the transformations by which nutrients taken from soil or air for constructing the materials that constitute the plant body are set free again in forms available for plant nutrition. Broadly speaking, one may regard the various elements of which a plant is composed as taking part in a recurrent cycle; an upgrade phase in which, as constituents of simple inorganic compounds, they are incorporated into more complex organic molecules, followed by a downgrade phase during which these complex molecules are disintegrated and the elements again become constituents of simple inorganic compounds.

Thus, carbon starts the upgrade part of the cycle in the form of atmospheric carbon dioxide; it is incorporated into more or less complex organic compounds by means of the energy green plants are able to absorb from light. The organic compounds so formed eventually undergo a series of downgrade changes with release of the energy used in their formation and with ultimate liberation of carbon dioxide gas. This final simplification may be reached by a number of different routes; some of the organic compounds in plant tissues, such as sugars, are broken down in part to carbon dioxide during respiration by the plant that produced them; most await the death and disintegration of the plant in the soil, where they undergo successive stages of breakdown by the activities of soil organisms with the final production of carbon dioxide (fig. 29). The downgrade part of the cycle may be prolonged by direct transference of organic substances with little or no simplification to the bodies of other organisms as occurs in saprophytes, parasites, plant-consuming animals and animal-consuming plants.

A similar cycle is gone through in respect to other elements. Phosphorus and sulphur, for example, are generally absorbed by vascular plants in the form of inorganic sulphates and phosphates; within the plant they are incorporated into proteins and other organic substances; on the death of the plant these

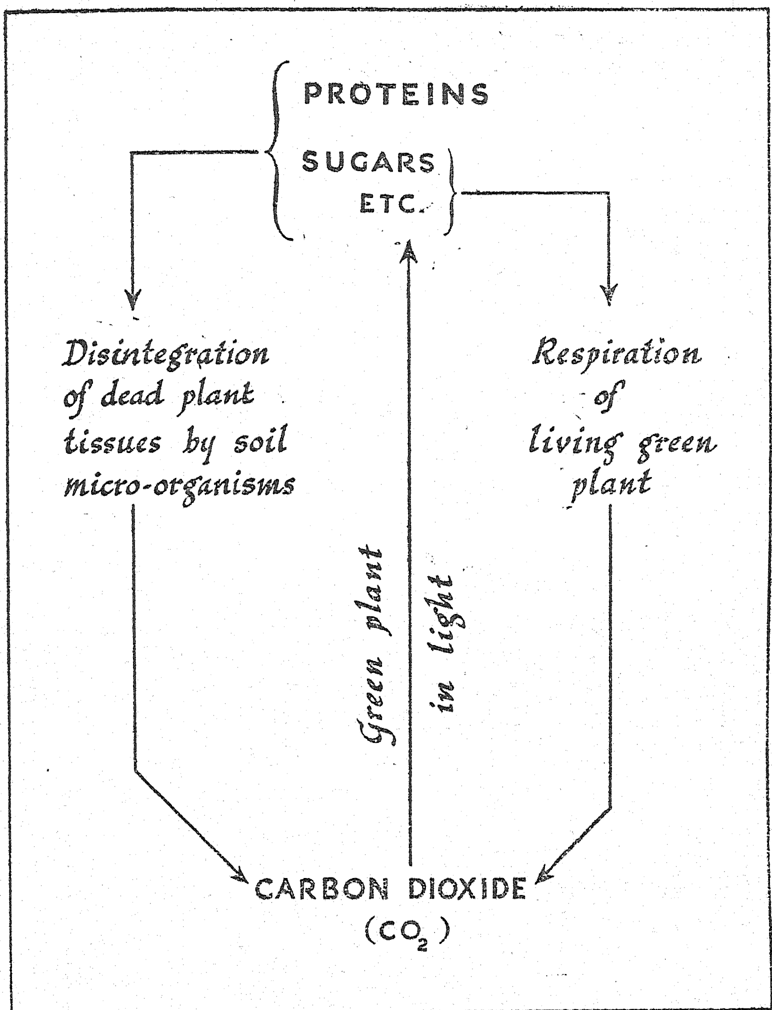


FIGURE 29
Diagram illustrating the 'carbon cycle' in its simplest form.

are broken down by soil organisms to yield again simple inorganic compounds of phosphorus and sulphur. As with carbon, the final simplification may be delayed by intervention on the part of saprophytes, parasites, etc.

The steps followed both in upgrade and downgrade phases, the details of the chemical changes involved, and the organisms concerned vary widely in different cases and under different conditions; there are still a great many details concerning these processes about which we know comparatively little, but the general nature of these cycles—the disintegration and simplification after death of the complex compounds constructed by organisms during their lifetime—is clear enough.

The nitrogen cycle

The element nitrogen occupies a rather special position in nutrition. Variations in the amounts of nitrogen compounds available for nutrition react on growth with a rapidity and to a degree exceeding those produced by any other essential element; moreover, under natural conditions, the amounts of such nitrogen compounds in soil are almost always below the optimum and so become limiting factors for growth. Owing to the relative poverty of available nitrogen compounds in the soil, the rapid return of these on the death and by the decay of the plants that have removed them is highly desirable. For these among other reasons, the nitrogen cycle is of special importance and has had much study bestowed upon it.

It is true that the atmosphere contains almost unlimited quantities of uncombined nitrogen gas, but equally true that this is useless directly as a source of food to ordinary green plants. Any processes whereby this unavailable atmospheric nitrogen can be made to form available nitrogen compounds and so help to relieve the prevailing shortage of nitrogenous food must further increase the possibilities for growth.

For higher plants the nitrogen cycle may be considered to start with the nitrates in the soil. These are absorbed by the roots, carried up to the leaves where the nitrogen is combined

with other elements to form organic compounds, the most complex of which are proteins. It would appear that this process is not directly dependent on the presence of light, since protein synthesis can be carried out in the dark and in parts of the plant devoid of chlorophyll. Since one of the essential conditions is a plentiful supply of carbohydrate, protein synthesis is indirectly dependent on light and is specially associated with leaves.

The downgrade part of the nitrogen cycle occurs during the decomposition of dead plant and animal remains in the soil when proteins and other nitrogen-containing organic compounds are finally broken down to yield nitrates. Certain definite steps can be recognized in this process of decomposition. To begin with there is a stage called *ammonification* in course of which organic nitrogen compounds are progressively simplified to ammonia or ammonium salts. This is brought about by many types of micro-organisms. The proportional parts played by fungi and bacteria partly depend on whether the soil is acid or alkaline, the former in general favouring fungal, the latter bacterial activities. The final stage in which ammonium salts are converted to nitrates is known as *nitrification*. It occurs in two steps involving the action of two highly specialized bacteria, *Nitrosomonas* and *Nitrobacter*, the first oxidizing ammonium salts to nitrites, the second nitrites to nitrates. The latter organism has been shown to be highly sensitive to the presence of chlorates, traces of which inhibit its activity and lead to an accumulation of nitrites. (Lees & Quastel: *Nature*, 155, 276, 1945.)

The organisms taking part in the processes of ammonification do not, of course, act from any altruistic motives: each finds in the substratum something of use for its own nutritive purposes and in course of utilization part at least of this nutritive material is converted into substances of simpler chemical composition; these are then seized upon by other organisms with the production of still further simplified products, leading to the ultimate production of ammonia or ammonium salts. This last stage of ammonification is then followed by nitrification. The fact that the ultimate products from this chain of reactions are necessary food materials for higher plants is in no way designed by the micro-organisms concerned in producing them. The whole

chain of reactions provides an example among the many instances in nature of the close interdependence of one kind of organism on another and of the successful organization of social life in a mixed population by a process of 'taking in one another's washing'. Incidentally, the two bacteria concerned in nitrification are noteworthy as being among the few organisms that, like green plants, can utilize carbon dioxide for constructing organic compounds; in their case the requisite energy is derived from chemical oxidations and not from absorption of light by chlorophyll.

This summary represents the nitrogen cycle in its simplest form. Shortening of the cycle results from the ability of some plants to use downgrade compounds of nitrogen before they reach the ultimate stage of nitrates. For example, many Flowering Plants can utilize ammonium compounds as freely as nitrates; even organic compounds that appear before ammonification is complete can be absorbed by them to some extent, but not, as a rule, in amounts that have any practical importance.

Elaboration of the cycle may occur as a result of the interpolation of some parasite or herbivorous animal into the chain of events described. In such case transformation of protein-nitrogen to nitrate-nitrogen on the death of the plant is delayed, the organic nitrogen of the plant being transferred instead to the parasite or animal, although simplification to nitrate eventually takes place on the death of the latter—unless further postponement is incurred by, for example, the herbivorous animal serving as food for some carnivorous animal, or by the complementary activities of carnivorous plants which can use the proteins of animal muscle as a souce of nitrogenous food.

The introduction of an animal stage into the cycle results in a further complication owing to animals using nitrogenous compounds for respiration and forming by-products that contain nitrogen such as urea. These nitrogenous substances excreted by animals during their lifetime suffer the same fate on reaching the soil as do dead plant and animal remains; they are seized upon by soil micro-organisms and enter on a series of degradation stages leading ultimately to the formation of nitrates, each stage resulting in the liberation of energy at the service of the

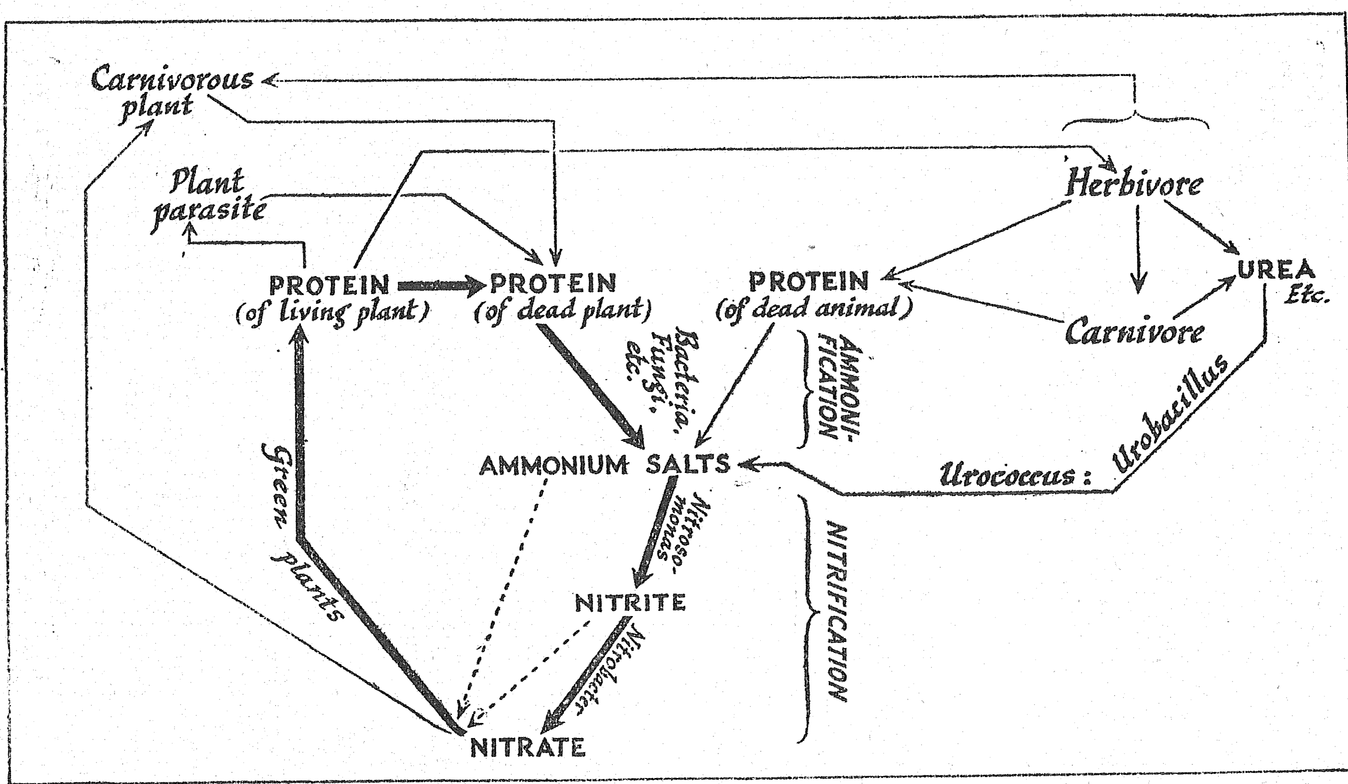


FIGURE 30

Diagram illustrating the 'nitrogen cycle' and some of its elaborations. Chemical substances are shown in Roman type, organisms in italics. The main nitrogen cycle is indicated by thick lines.

organism responsible for it.[1] An attempt to represent these steps diagrammatically is made in Fig. 30.

As described, the nitrogen cycle forms a closed system; the amount of nitrogen present in combined forms is constant throughout although the complexity of the compounds incorporating it varies. The uncombined molecular nitrogen of the air is outside the system because the organisms concerned in the cycle can make no use of it. There are, however, a number of natural processes that result in addition of nitrogen to the cycle, or subtraction of nitrogen from it: that is to say, there are processes that bring the inert nitrogen gas present in the atmosphere into some form of chemical combination that can enter the cycle, or that lead to the escape of molecular nitrogen from chemical combinations existing within it.

Nitrogen fixation

Of the additive processes, the simplest is the purely physical one by which nitrogen and oxygen in the air are combined under the influence of atmospheric electrical discharges to form oxides of nitrogen; these, washed down by rain, can be used directly by green plants. The amounts of available nitrogen compounds introduced into the nitrogen cycle in this way are not large. Measurements at Rothamsted Experimental Station over a five-year period showed an addition of 4·4 pounds of nitrogen per acre per annum to the soil from the rain, but part of this is to be accounted for by atmospheric ammonia, so that the gain in nitrogen compounds from nitrogen fixation is considerably below this figure. On the other hand, the availability of cheap and plentiful electric power has led to extensive production, artificially, of nitrogen compounds from the nitrogen of the air for use in agriculture and industry.

[1] For example, urea, $CO(NH_2)_2$, is hydrolyzed by the bacteria *Urobacillus pasteurii* and *Urococcus ureae* to ammonium carbonate, $CO_3(NH_4)_2$, which is then oxidized to nitrite and nitrate by *Nitrosomonas* and *Nitrobacter* respectively.

Far and away the most important processes in nature whereby the nitrogen of the air is caused to combine with other elements to form compounds available for plant nutrition depend on the activities of micro-organisms. Such organisms are termed *nitrogen-fixing* organisms and the process is referred to as *nitrogen fixation*.

Many bacteria and a number of fungi have been claimed as possessing the power to fix atmospheric nitrogen in some degree, but in most instances, under the experimental conditions employed, the amount so fixed is quite small. Two genera of free-living soil bacteria, however, stand out as possessing this property to a high degree, *Azotobacter* and *Clostridium*, the former preferring aerobic and the latter anaerobic conditions. Without question, under favourable soil conditions, either of these bacteria is capable of adding considerably to the total amount of nitrogen compounds in the world available for plant nutrition.

Of even greater practical importance as nitrogen-fixers than the above two free-living soil bacteria are certain micro-organisms that can live in partnership within the tissues of other plants. The best known of these are the bacteria that give rise to and then inhabit the swellings or 'nodules' of leguminous plants. These have had various names bestowed upon them; *Bacterium radicicola* was one of the earliest when it was assumed that a single species was involved; *Pseudomonas radicicola* was used by Moore in the belief that the organism has only a single flagellum; later work has shown that several forms, if not several species, are concerned, and names such as *Rhizobium leguminosarum*, *Rh. trifolii*, *Rh. phaseoli*, etc., have been used for the bacteria capable of forming nodules in particular leguminous species. All that we need concern ourselves with here is that a species of bacterium having several forms, or a number of closely related bacterial species, are able to invade the roots of leguminous plants by way of the root-hairs, and whilst growing within the tissues are able to 'fix' considerable amounts of nitrogen (i.e. to form nitrogen compounds from atmospheric nitrogen) which can be utilized by the leguminous host. A proportion of these nitrogen compounds escape from the roots into the soil

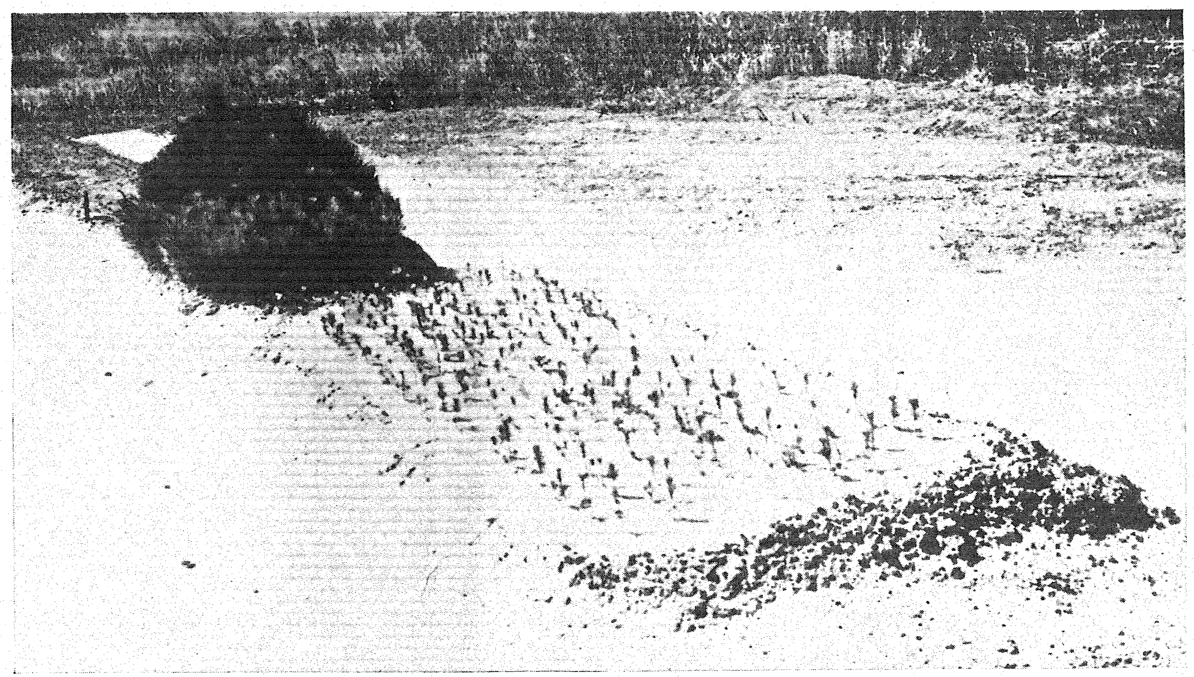
and benefit other, not necessarily leguminous, plants in the near neighbourhood. The bacteria obtain the energy necessary for nitrogen fixation from the carbohydrates supplied by the leguminous plant. A co-operative partnership of this kind between two organisms is described as *symbiosis*.[1]

A certain number of plants belonging to other families form nodules of a similar kind on their roots, among which may be mentioned Alder (*Alnus*, spp.), *Eleagnus*, Bog Myrtle (*Myrica Gale*) and the She-oak (*Casuarina* spp.); it appears from culture experiments that nitrogen fixation occurs in these cases also, although it is probable that the bacteria concerned are not in all cases, if in any, identical with those present in the nodules of the leguminosae, nor the same in all the plants mentioned. In one tropical genus, *Pavetta*, and a few others, nodules are formed in the leaves instead of in the roots; these also contain bacteria which have apparently the power to fix nitrogen. The available evidence suggests that the bacteria associated with leaf nodules are different from those found in any of the root nodules.

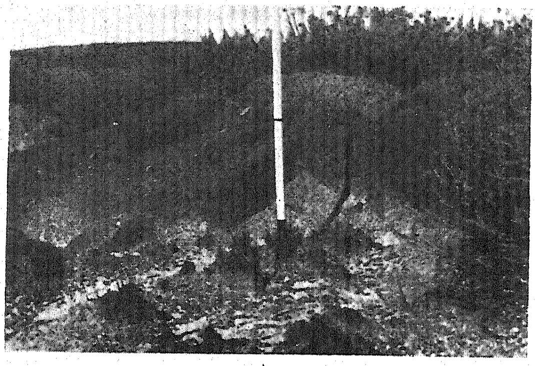
It is clear that considerable quantities of nitrogen compounds may become available to plants through the agency of nitrogen-fixing bacteria that are able to use molecular nitrogen when living, not as free organisms in the soil as do *Azotobacter* and *Clostridium*, but within the tissues of other plants with which they form a symbiotic partnership. Members of the Pea family are outstanding for the two reasons that almost every species can form such an association and also in respect to the large amounts of nitrogen fixed by the associated bacteria.

No satisfactory evidence has been obtained hitherto that the bacteria inhabiting the nodules of any of these plants, even those of members of the family leguminosae, are able to fix nitrogen except when living in association with a Flowering Plant. The bacteria can be grown successfully on culture media apart from their hosts, but do not fix nitrogen under these conditions. There are also strains of bacteria that form nodules but do not fix nitrogen. The interesting observation has been made that nodules containing bacteria that are effectively fixing nitrogen are sometimes distinguished by being coloured red owing to the

[1] Virtanen, A. I. 'Symbiotic nitrogen fixation.' *Nature* *155*, 747, 1945.



8. Effect on the growth of a plant of supplying its mycorrhizal fungus when this is lacking from the soil. Two beds of seedlings of a Himalayan species of pine (*Pinus longifolia*) from the same sowing in Northern Rhodesia. Further bed inoculated with soil containing a mycorrhizal forming fungus for the species from a vigorous plantation of this pine at a station in Southern Rhodesia, 1,000 miles distant; nearer bed untreated.



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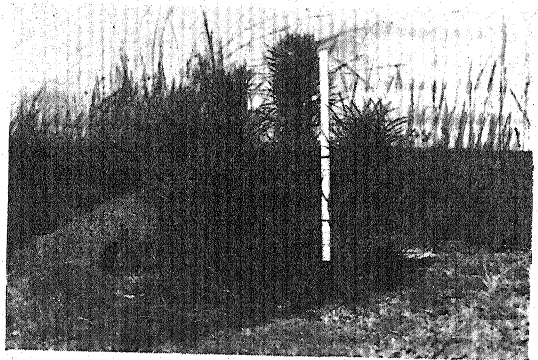

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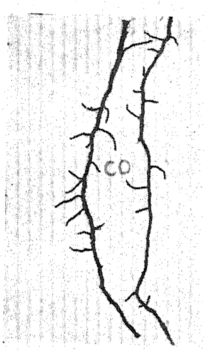

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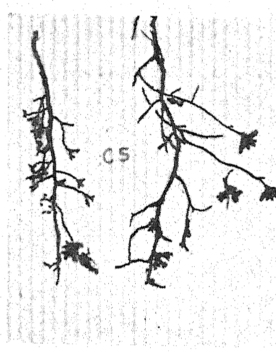

D

9. Effect on the growth of a plant of providing conditions in which its mycorrhizal fungus, present in the soil, can become active. (A) Patch sowings of Corsican Pine in Wareham Forest, Dorset, seventeen months from sowing: untreated. (B) ditto, but treated with 2 lb. of an organic compost per patch at sowing. (C) Condition of roots of plants from untreated patches ten months after sowing: mycorrhizas sparse or lacking. (D) Condition of roots from treated patches ten months after sowing: profuse development of short roots that have become mycorrhizas.

production of haemoglobin, the pigment of the red blood corpuscles of animals.[1 2] It is of considerable interest that plants should be capable of producing a substance so characteristic of animals.

This does not exhaust the subject of nitrogen fixation, however, since the greater proportion of Flowering Plants and many non-Flowering Plants form more or less definite partnerships with soil fungi. This partnership was first recognized in the roots of trees by the German botanist Frank in 1885; since then, a majority of the higher plants have been found to be capable of forming this association. The specialized roots containing the fungus partner, often readily distinguishable from ordinary roots by their external appearance, are given the name of *mycorrhizas* or 'fungus-roots'. Lower plants such as Liverworts which do not produce true roots also form associations with fungal hyphae.

The possible nutritive significance of mycorrhizal associations will be discussed later; the point of interest at the moment is that in some few cases, for example, in heaths and orchids, there is experimental evidence that nitrogen fixation occurs, although this capacity is still the subject of controversy and must be regarded as probably exceptional on the part of mycorrhizal fungi.

A capacity for effective nitrogen fixation has also been claimed on good evidence for certain primitive algae, for example species of the genus *Anabaena* belonging to the Blue-Green Algae. Among places in which these algae are found is the soil of rice fields and the evidence points to them being important agents of nitrogen-fixation here.[3]

The diagram in fig. 31 attempts to indicate the ways in which these nitrogen-fixing processes that add to the world's supply of nitrogen compounds are related to the main nitrogen cycle.

[1] Keilin, D. and Wang, Y. L. 'Haemoglobin in the root nodules of leguminous plants.' *Nature, 155*, 227, 1945.

[2] Virtanen, A. I. and Laine, T. 'Red, brown, and green pigments in leguminous root nodules.' *Nature 157*, 25, 1946.

[3] De, P. K., The role of blue-green algae in nitrogen fixation in rice-fields. *Proc. Roy. Soc., 127B, 121, 1939.*

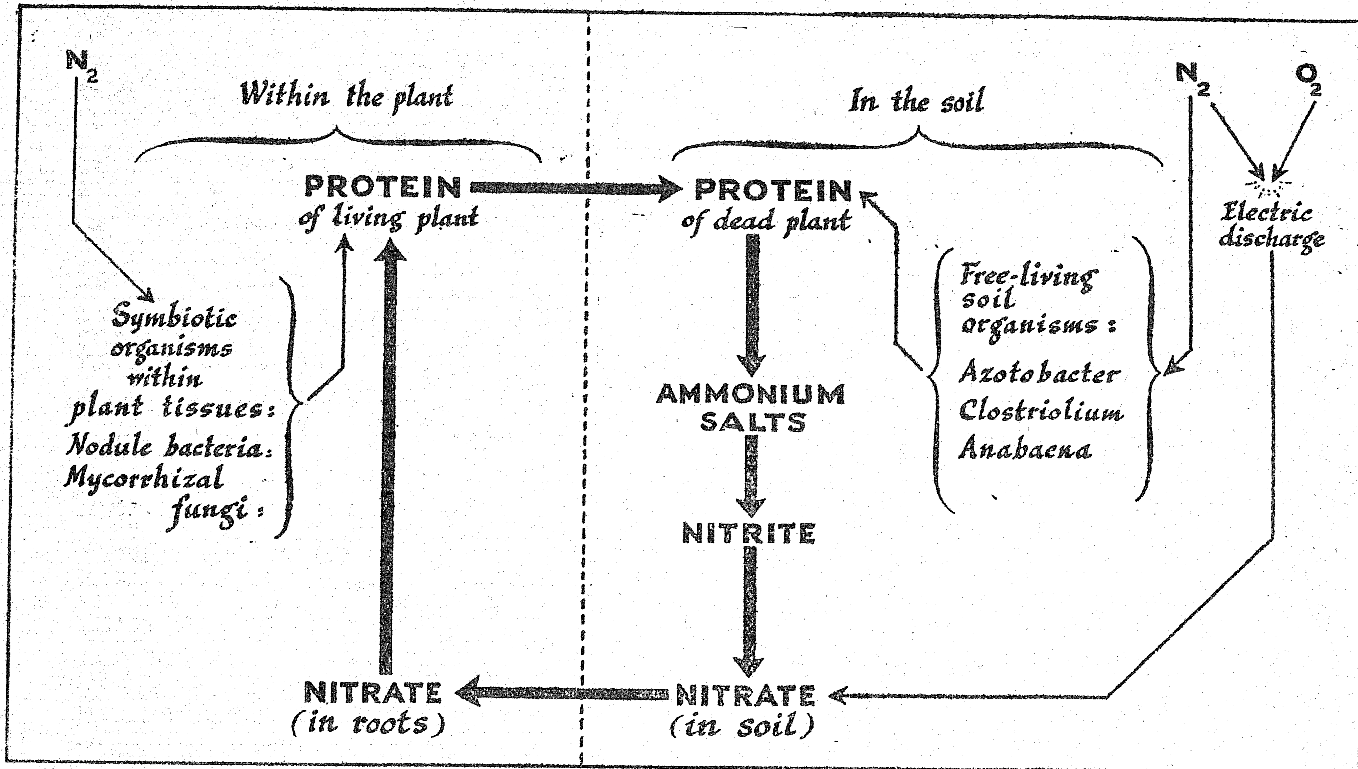

FIGURE 31

Nitrogen-fixation: Diagram to illustrate the chief ways in which atmospheric nitrogen, useless for the direct nutrition of most plants, may be introduced into the nitrogen cycle and incorporated into nitrogen compounds which then become generally available as a source of nitrogenous food.

Denitrification

Besides being responsible for the conversion of one nitrogen compound into another or for increasing the total sum of nitrogen compounds in the world by fixation of atmospheric nitrogen, bacteria may in some cases set free the nitrogen from compounds containing it as molecular nitrogen, i.e. as nitrogen gas. These are known as *denitrifying* bacteria and their activities lead to loss in the total of nitrogenous nutrients available for the majority of organisms.

Denitrification is often as much a result of the conditions of growth as of the presence of special kinds of bacteria. In the absence of adequate supplies of oxygen, for instance, many bacteria can obtain the oxygen they require from such substances as nitrates, retaining the oxygen and setting free nitrogen as molecular nitrogen. The removal of nitrogen from nitrogen compounds and hence from accessibility as food material to most organisms in this way must be distinguished from loss of nitrogen from a soil in the form of ammonia. The latter process impoverishes in available nitrogen compounds the particular soil in which it occurs, but the world supply is unaffected since the ammonia diffusing into the air is eventually washed down in rain somewhere else. From the point of view of the farmer who owns a piece of land, both these processes lower the fertility of his soil and are equally to be deplored; that the ammonia lost from his fields, unlike the nitrogen liberated by denitrifying organisms, is deposited elsewhere and is not a permanent loss from the soil as a whole is, indeed, a distinction of no practical interest to him! While losses of either kind cannot be altogether prevented, undoubtedly they can be decreased. Poor aeration of the soil will obviously favour those of the first kind; soil treatments that favour production of ammonia, such as heavy dressings of farmyard manure on an alkaline soil, encourage losses of the latter kind.

The soil population

Leaving those aspects of nutrition concerned specially with nitrogen and returning to those relating to the soil in general, it is evident even from the rapid survey given that utilization of humus for plant food involves far more complex processes than does that of artificial manures in the form of inorganic mineral salts. The latter are immediately accessible, but since many go rapidly into solution, appreciable amounts tend to be lost in the drainage water before plant roots have time to absorb them. The humus, on the other hand, breaks down slowly so that the roots are provided with available food substances steadily over a long period instead of with at first a surplus greater than they can absorb and later with less than they might make use of. Moreover, the presence of humus checks losses in the drainage water, humus having in a high degree a capacity for holding or 'adsorbing' salts in solution; for this reason an adequate proportion of humus in the soil is highly desirable even when reliance is placed on artificial manures for the supply of nutrients.

Because humus provides food for the numerous micro-organisms that contribute to its breakdown, its presence makes possible the existence of an extensive micro-flora and micro-fauna, including nitrogen-fixing bacteria, mycorrhizal fungi, protozoa and nematodes, as well as earthworms and larger animals, some obtaining nutriment from the humus or products of its decomposition, others by preying upon fellow-members of the soil population. All of these activities affect profoundly the character of the soil and the growth of higher plants in it.

The effect on soil fertility of the activities of one member of the soil population, namely earthworms, was emphasized by Charles Darwin. Recent work in America has provided further evidence of the importance of these animals.[1] It was shown, for example, that worm casts contained five times as much phosphate and eleven times as much potash in a form suitable for absorption by roots as do the upper layers of soil. It might be

[1] Lunt, H. A. and Jacobson, H. G. M. 'The chemical composition of earthworm casts.' *Soil Sci.*, *58*, 367, 1944.

expected, therefore, that increase in the worm population would be followed by increase in plant growth due to the additional nutrients brought into soil layers normally occupied by the feeding roots of plants, apart from any benefit resulting from the improved aeration produced by worm burrowings. Sensational claims have been made as to the beneficial effects that have followed the large-scale introduction of suitable worms to raise artificially the natural worm population. It is too early to judge the success or otherwise of such soil treatments, but that they are regarded seriously by many cultivators is indicated from the fact that in California and elsewhere 'worm farms' have been established to supply worms on a commercial scale.

Mycorrhizal fungi

The part played by mycorrhizal fungi (p. 145) calls for some additional consideration in view of the special relationships involved.

Like many other fungi they live saprophytically upon the organic material in the soil—breaking down the plant and animal residues of which it is composed in the course of extracting nutriment for themselves.

Fungi are most easily identified by the characters of their spore-bearing structures or sporophores and the structure of their reproductive bodies or spores. The identity of many of these mycorrhizal fungi has been established and in a number of cases they have been isolated from their surroundings and their relationship with their hosts proved by bringing together fungus associate and host under completely controlled pure-culture conditions, i.e. growing them on artificial media free from contamination by any other organism. More especially is this the case in certain groups of plants in which the mycorrhizal habit is conspicuous and has long attracted the attention of botanists.

In one type of association the fungus forms conspicuous coils *within* the cells of the root, often in a restricted part of the cortex. Such *endotrophic* mycorrhizas may not be easily distinguishable

from ordinary roots externally, the presence of the fungus being revealed with certainty only on microscopic examination of a root section.

In Ericaceae, the family to which the Heaths and Heathers belong, the endotrophic root fungi can be extracted and grown in pure culture; from the characters of the reproductive bodies formed they are considered to belong to the genus *Phoma* and to be closely allied to certain well-known plant parasites. In Orchids, the fungi can also be extracted and grown in pure culture, but although much is known about their appearance and behaviour, their systematic position and relationships with other fungi is still somewhat uncertain. In a very large number of Flowering Plants, extending to something over 80 per cent of those known to botanists and in some of the lower plants allied to the Ferns, the identity of the endotrophic root-associates is still uncertain. These mycorrhiza-forming fungi are very widely distributed in soils all over the world; they show many features in common and evidently belong to a single group or to several groups very closely allied. Ignorance of their systematic position is due to the fact that they do not produce spores when associated with plant roots and efforts to isolate and cultivate them apart from their hosts have been unsuccessful.

It is the mycorrhizal fungi of certain trees that are most easily recognized by those who are not botanists.[1] Many conifers such as Pines, Spruces, Larches and their relatives, as well as Oak, Beech, Hornbeam, Chestnut, and allied tree species, form mycorrhizal associations with common fungi of woodland and forest soils, the conspicuous sporophores of which under the names of toadstools, puff-balls and the like are well known to everyone, especially during the autumn months. Members of the same or other groups of the Higher Fungi allied to the Puff-balls and Truffles and forming subterranean sporophores are also mycorrhizal associates of trees. In these mycorrhizas the mycelium ramifies in the intercellular spaces without as a rule entering the cells and invests the short roots with an interwoven external sheath or *mantle*. Mycorrhizas of this *ectotrophic* type are readily distinguishable externally from ordinary roots, being of larger

[1] Rayner, M. C. *Trees and Toadstools.* Faber and Faber, 1945.

diameter and of varying colour due to the presence of the enveloping mantle.

In the case of some of these mycorrhizal fungi of trees, it is believed that sporophores are produced only when they are growing in symbiosis with their host trees and disappear when the trees are felled. In other words, these fungi are unable to complete their life cycles unless the association is established. Reciprocally, the host plant may show dependence on the presence of its mycorrhizal fungus at some stage of development.

The Common Heather or Ling (*Calluna vulgaris*) has minute seeds that when shed carry threads of the endotrophic root fungus upon their seed coats and the seedlings show arrest of growth at a very early stage unless fungus infection of the seedling tissues takes place. Orchids behave in a similar manner although the fungus is not carried on the seed coat and infection of the young seedling must take place from the soil. The fact that it has been found possible to provide the requisite stimulus to seedling development by artificial means, such as controlling the acidity of the surroundings and providing a supply of sugar for the developing seedling and that many orchid growers now use these methods commercially, does not in any way invalidate the facts that have been established in respect to the importance in nature of proximity to the appropriate fungus at germination. In the case of trees, in which both endotrophic and ectotrophic types occur, there is overwhelming evidence that vigorous growth is associated with profuse mycorrhizal development and poor growth with the absence of this, but there are still divergent opinions about the exact role played by the fungus. Many examples might be cited of seedbeds and plantations of conifers in which the young trees showed almost complete arrest of growth at an early stage, recovering their vigour only after the introduction of suitable mycorrhiza-formers if such are lacking, or the application of soil treatments which invigorate the mycelium of such fungi if already present but unable to form associations. The result of successful treatments is a profuse production of normal fungus-roots or mycorrhizas with renewed vigour of growth on the part of the trees (Pl. 8, 9; facing p. 144, 145.)

Much remains to be learned about the mechanism of exchange between trees and their root fungi. The formation of mycorrhizas and the hyphal threads associated with them increases the area of surface over which absorption into the roots can take place. It must be remembered also that fungi can use organic sources of nutriment in the humus inaccessible to the roots of the higher plants. There is conclusive evidence that certain mycorrhizal fungi cannot form the growth-promoting substances required for their full development and must obtain these from their hosts. There is evidence also that the host trees may benefit in a similar manner; it has been asserted, indeed, by certain workers that mutual exchanges of this kind represent the most important aspect of mycorrhizal relationships in trees. However this may be, there is no doubt in the case of trees that reciprocal exchanges beneficial to both partners take place or that the fungi concerned play an overwhelmingly important role in maintaining the fertility of woodland soils. It is clear also that the establishment and stability of this balanced partnership or symbiosis between trees and their root fungi follows upon the presence of humus and depends upon soil conditions favourable to the healthy growth and proper functioning of both partners. It also appears probable that failure to establish a relationship with an appropriate mycorrhizal fungus lays the roots open to more ready attack by pathogenic soil fungi.

Soil ecology

The conditions present in a well-aerated soil containing humus permit the interrelated activities of a vast number of soil organisms. It is in such an environment that the roots of higher plants grow naturally, subjected to competition for food materials but at the same time provided with nutritive substances arising from death and decay of other members of the soil population and free to absorb their secretions whilst these were still living. Reduction in the amount of humus or disturbance of the physical or chemical characters of the soil bring about alteration of balance in the activities of members of the soil population or may even bring these activities to an end.

The biological interrelations we have been considering have been concerned, directly or indirectly, with nutrition. There are, however, important reactions between members of a soil population unconnected with nutritive processes.

For example, the roots of a plant not only absorb water and food materials; they also excrete substances. Among the latter carbon dioxide, arising as a by-product of respiration, is prominent and serves the useful purpose of bringing into solution nutritive substances in the soil that are only slightly soluble in pure water. The root nodules of leguminous plants have been mentioned earlier as excreting nitrogen-containing substances that may be of use to neighbouring plants (p. 143); no doubt a great variety of organic and inorganic compounds escape from roots into the surrounding soil although not usually in amounts that render them of importance.

Apart from substances, that may or may not possess nutritive value for the growing plant, some excretory products, even in minute traces, are capable of exercising a profoundly depressant effect on the growth of other organisms. The evidence that Flowering Plants can curtail the growth of their competitors in this way, while not lacking, is not extensive or in general precise; on the other hand, the widespread ability of lower plants to produce growth inhibitors is well recognized. Such substances are given the general name of *antibiotics* and vary from generalized depressants like the alcohol produced by yeast or the citric acid produced by the fungus *Citromyces* to highly specific substances that affect a small range of organisms only. In all such cases, a low susceptibility to the antibiotic substance is shown by the organism producing it, so that competition for food materials on the part of more susceptible organisms is to a greater or less degree eliminated.

A case that has recently caught the public imagination owing to its practical therapeutic applications is the antibiotic substance penicillin produced by the mould fungus *Penicillium notatum.* Minute traces of penicillin check the multiplication of a large number of bacterial species, among them many pathogenic forms, mainly those in the category known as Gram-positive. At the same time, penicillin has a low toxicity towards the cells of

human tissues. These two facts together are responsible for the sensationally successful results obtained from the use of penicillin in many diseases caused by species of bacteria susceptible to it, the penicillin preventing the bacteria that have succeeded in invading the tissues from multiplying beyond the capacity of the leucocytes of the blood to destroy them. The main difficulty in its medicinal use is to maintain sufficient penicillin in contact with the attacked tissues owing to the rapidity with which it is carried away in the blood-stream and eliminated from the body.

The successful use of penicillin in combating disease is further limited by the fact that many pathogenic bacteria, even in the Gram-positive class, show little sensitiveness to it.

Many of the substances excreted by organisms other than *Penicillium notatum* are powerful antibiotics; few of those yet investigated, however, possesses the low toxicity to human tissues that makes penicillin so valuable an addition to the curative agents available to medical science.

Penicillium notatum is a soil organism and the fact that so many components of the soil micro-flora can and do produce antibiotic substances more or less specific in checking the growth of other organisms must be an important factor in determining the balance of the soil population. Furthermore, a change in physical or chemical conditions which may not affect some organism directly, may yet indirectly affect it profoundly owing to the changed activity induced in other antibiotic-producing species.

One of the beneficial roles performed in symbiotic associations may well be the production of antibiotic substances by one partner which serve to protect the other from pathogenic attack. Something of the kind may exist in tree mycorrhizas, since failure of the roots to establish a normal relationship with a mycorrhizal fungus may lead to the formation of undesirable associations harmful to the higher plant.

It is the presence of humus that renders the conditions for plant growth so infinitely more complex in soil than in water or sand culture, for humus is the ultimate source of the nutriment that makes possible the existence of the soil micro-population.

Whilst the addition of, say, ammonium sulphate to a water

culture may mean little more than providing the roots of the plants in the culture with a larger amount of available nitrogen, its application to soil may have the further effect of disturbing the normal balance between the members of the soil population; this may react indirectly on plants growing in the soil by modifying in some way the micro-biological activities on which the sustained fertility of the soil depends. Whether changes so induced may be for better or for worse is not part of the present argument, the purpose of which is to emphasize that the effects of treatments applied to a plant growing in soil cannot be compared with the comparatively simple effects that follow their use in water or sand cultures where reactions on a micro-population can be ignored—they are infinitely more complex and far-reaching. The more fervid advocates of the extensive use of artificial fertilizers are sometimes apt to forget, ignore or underrate the results of disturbing the micro-biological balance in the soil.

Humus possesses certain physical properties that greatly influence soil characteristics, quite apart from the foregoing complexities of a biological nature to which its presence in soil gives rise. Chief of these are the increased water-holding capacity and improved aeration associated with the presence of humus, the cellular structure of plant tissues giving a sponge-like character to their remains that tends both to hold water and keep the soil open. This sponge-like texture is enhanced by the formation of cavities where plant fragments have disappeared as a result of their decay. The aerating effect is still further increased by the activities of earthworms and other small animals that burrow through the soil. Moreover, especially in the later stages of decomposition, the humus particles possess a large total surface which confers on the whole considerable powers of adsorption—the property of holding soluble substances on the surfaces of the particles—and so tends to prevent wastage and loss of soluble nutrients in the drainage water. These same final products of decomposition also behave as a cement holding together the finer mineral particles and so leading to the production of the crumb structure or 'tilth' that is so characteristic of an easily worked fertile soil, even when the constituent mineral basis consists largely of fine particles of clay. In the absence of

humus, such a soil is waterlogged in wet weather, brick-hard when dry, rendering it at almost all times difficult or impossible to cultivate and unfavourable as a medium for the growth of most organisms apart perhaps from some anaerobic bacteria. The physical characters imposed on soil by the presence of humus are obviously of considerable importance in the practice of agriculture as well as under natural conditions.

The complex balance of biological activities we have considered at some length in this chapter not only affect nutritive relations, but react also on the physical character of the residues formed; conditions that check or drastically modify bacterial and fungal action not only bring to an end the liberation of available food materials from the humus, but result also in waterlogging and defective aeration. It is evident therefore that both the physical and nutritive characteristics of a soil are greatly influenced by the presence of humus and by the course of events followed during humus decomposition; this is dependent upon the conditions of the environment and the nature and activities of the micro-organisms present, which in turn are interrelated with the nutritive materials derived from the humus.

In ascribing a role of this importance to humus, it is not forgotten that a very wide range of physical properties may result from variation in the proportions of the different-sized inorganic particles that compose the greater bulk of most soils. In those soils with a low humus content indeed, these factors may be of predominant importance in deciding the physical nature of the soil; in nature such soils are almost invariably of limited fertility owing to their curtailed microbiological activity and if used for the production of crops require some form of artificial treatment, either by continuously supervised addition of inorganic nutrients or by addition of organic residues which will permit the establishment of a sustained self-regulating biological system.

Sufficient has been said, it is hoped, to show that the problems connected with plant growth in soil are not only chemical and physical but also biological, that is to say, they are, in the broadest sense, *ecological*. The soil is not merely a convenient inert medium in which the lower ends of trees and other plants are sunk so that the stems are held upright like telegraph poles, nor

is it to be regarded merely as a sort of sponge holding a supply of the water and mineral salts necessary for plant nutrition. Below ground, in the soil, is a world with a life of its own, comparable with the world above ground. The activities of this soil population must be taken into account in any problems concerned with growing plants in soil. One of the dangers attending the use of artificial fertilizers that must be constantly kept in mind is that an application of some inorganic substance that is of direct nutritive value to the crop plant may cause a disturbance in the balanced relations of the soil population that reacts ultimately unfavourably on the crop plant and on the physical character of the soil.

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Chapter 7

POLLINATION, FERTILIZATION AND PARTHENOGENESIS

In Flowering Plants an important stage in sexual reproduction is *pollination*, that is, the transference of pollen grains from anther to stigma of the same or another flower. This transference may be brought about by various agencies, especially by wind currents and by insects of various kinds, less frequently by water, by other animals such as humming birds, or by some mechanical device within the flower itself. Volumes might be, and indeed have been written describing the numerous and remarkable structural features in flowers concerned with the bringng about of pollination. (E.g., *The different forms of flowers on plants of the same species*, and *The effects of cross and self fertilization in the vegetable kingdom* by Charles Darwin.)

The pollen grain, having reached the stigma by one means or another, germinates to form a pollen tube which grows as does a parasite down the style towards the ovary containing the ovules, one of which it enters. Eventually, a nucleus from the pollen tube fuses with the nucleus of the egg-cell contained within the ovule; this fusion process is known as *fertilization.*

The fertilized egg-cell then proceeds to grow into the embryo of a young plant of the next sexual generation. Without the stimulus derived from union with the male nucleus from the pollen tube, the egg-cell is normally incapable of developing. It is true that in Lady's Mantle (*Alchemilla vulgaris*), the Hawkweeds (*Hieracium* spp.) and some other plants an embryo is regularly produced in the absence of fertilization, a phenomenon

known as *parthenogenesis*; but such behaviour is exceptional and may be ignored for present purposes.

The Seed

Development of the fertilized egg-cell into a new plant is not a continuous process. After fertilization, the whole ovule undergoes enlargement and on reaching a certain stage of develops ment loses much water; growth of the embryo within slow-down and ceases; the ovule has become transformed into the resting seed. It contains an embryo in a state of arrested development; within or around the embryo is a supply of food material available for its future growth; the whole is surrounded by a protective envelope—the seed-coat. If a seed is placed under conditions suitable for germination, the embryo may resume its growth at once, produce a seedling and in time a mature plant. In some cases, as already described (p. 96), some special stimulus may be needed to arouse the embryo from the dormancy that overtakes it when the seed ripens.

The development of dormancy in seeds is associated with the loss of water that occurs in the later stages of ripening and it is sometimes possible to avoid the full onset of the dormant phase by removing the seeds and sowing them before they are fully ripe. Thus, the seeds of many species of *Primula* are notoriously slow to germinate if sown when mature and dry, often germinating sporadically in the seed-pan a year or more after they have been sown; if removed from the capsules before they have become dry and sown immediately, they often germinate without delay. In this way it may be possible to avoid the delay in germination caused by changes in seed-coat and embryo during the later stages of ripening of the seed.

Longevity of seeds[1]

We have considered ways in which the dormancy of seeds

[1] Crocker, W. 'The life-span of seeds.' *Bot. Rev.*, *4*, 235, 1938.

may be overcome (p. 96), but not the converse problem of how long the embryo of a seed can remain dormant without loss of vitality: to put the matter more directly, how long seeds can be kept without losing their capacity for germination.

Seeds differ widely in this respect; some lose their vitality within a few days; those of a majority of plants have a life-span of three to fifteen years, some have germinated after more than one hundred years of storage. Any statement about this matter must allow for the fact that the life-span of seeds depends not only on the kind of plant producing them but also on the conditions under which they are stored.

Among plants whose seeds have a short life-span are the species of grass known as Wild Rice (*Zizania aquatica*), Willows (*Salix* spp.) and Poplars (*Populus* spp.). Seeds of the first lose their vitality if they are allowed to dry in the air for even a few days, retaining it until spring if kept in water at about freezing point. Seeds of Willow, on the other hand, whilst rapidly losing vitality when allowed to dry in the air, may give 50 per cent germination after a year if quickly and thoroughly dried and stored in closed tubes. Loss of water appears to be the injurious factor in the first case but some other cause must be responsible in the second. Sugar Cane seeds degenerate so rapidly when stored fully exposed to air that they cannot be shipped to distant sugar-growing districts with certainty that they will germinate on arrival. Their vitality can be materially lengthened by drying thoroughly, sealing in tubes and storing at freezing point.

The majority of seeds have a medium life-span of three to fifteen years. Most of these endure complete desiccation and store best in this condition. Sealing hermetically, resulting in exclusion of oxygen and accumulation of the carbon dioxide of respiration, also tends to prolong vitality, as does storage at a low temperature. How far from being harmful is a temperature near freezing point (i.e. 0° C.) is shown by the fact that many seeds *when completely dry* may be immersed in liquid air (—186° C.) for considerable periods without harm; at temperatures such as this, respiration and other vital activities must virtually cease.

There are certain plants the life-span of whose seeds is so long that they form a class by themselves. The record longevity supported by documentary evidence is probably held by one of the Sennas, *Cassia multijuga*, seeds of which germinated after storage for 158 years in the National Museum of Paris. Most records of this kind are of necessity derived from seed taken from old herbaria and collections; a number of cases are on record of seeds germinating 80 to 100 years after collection, for example, those of *Mimosa glomerata*, *Cytisus biflorus* and *Cassia bicapsularis* and others after fifty years. As already mentioned, most, although not all of these long-lived seeds belong to leguminous species; all have relatively impermeable seed-coats, so providing two conditions, exclusion of water and oxygen, conducive to long vitality.

Evidence of a different and more unusual kind is available in the case of the Indian Lotus, *Nelumbium nucifera*. Documentary evidence that the seeds of this plant remain alive for at least 150 years is provided by specimens from the herbarium of the British Museum. Even more surprising data have been obtained from seeds buried in a naturally drained lake bed in southern Manchuria. These seeds lay buried four to five feet deep in the old lake bed. The eroding river which drained this lake cut a deep channel through the lake bed, which, now dry, carries trees and is partly under cultivation. From the rate at which the river is eroding its bed, the age of the trees, and the historical record of farming operations, it has been computed that it must be at least 120 years, more likely 200 to 400 years, since *Nelumbium* could have been growing there and so have produced seeds. These seeds still give perfect germination after the hard impervious coats have been broken. The claim that germination has been obtained of mummy wheat grains thousands of years old from Egyptian tombs has long since been shown to be without foundation.

Less sensational but of more practical interest are records now in course of accumulation at various research stations as to the fall in germination capacity from year to year of seeds of commercial importance under different methods of storage. Many seeds lose vitality in the course of a few years under the best

storage conditions, the majority have a life-span of under twenty-five years. Those engaged on this research may therefore hope to see a considerable body of data collected within their own lifetime.

Another important aspect of this subject relates to the difficulty of eradicating those farm weeds, seeds of which can remain in a dormant condition buried in the soil for many years. When cultivation brings such seeds to the surface they may germinate and so provide fresh centres of weed infestation. This is one reason why systematic and continuous weeding is so important; if weeds of certain species such as Charlock (*Brassica sinapis*) are allowed to seed, the harm from one year's neglect may be operative for several years to come; it cannot be made good by more intensive weeding the following year.

Self- and cross-pollination

Returning to the part played by the flower in sexual reproduction, there are a number of interesting facts relating to control of the kind of pollen that reaches the stigma of any flower. As is well known, in general these controls operate in such a way as to favour pollination of a flower with pollen of the same species; but at the same time to favour pollination with pollen from an other plant, or at least from another flower, of the species; in short, to favour cross-pollination within the species.

By virtue of their different forms and colours and the different times of day at which they open, flowers attract different kinds of pollinating insects. Any plant species is thus likely to be visited by a comparatively small range of insects, sometimes by one kind only as happens in the Figwort (*Scrophularia nodosa*) which is pollinated almost exclusively by wasps. Even when a particular kind of insect is in the habit of visiting the flowers of several kinds of plant it tends to confine its visits to one species for considerable periods; no doubt it conduces to efficiency in the collection of nectar or pollen to avoid the frequent adjustment of movement that would be called for by visits to different types of floral structure.

On the whole, therefore, pollination by insects is more likely to result in the carriage of pollen between flowers of the same species than between those of different species, although the latter may occur. The distribution of wind-borne pollen is, of course, quite fortuitous except for its limitation to a definite flowering period which often falls early in the year before many insect-pollinated flowers are open.

The favouring of cross-pollination within the species can be brought about in numerous ways. The most effective is for the plants to be unisexual with male and female flowers borne on different plants as in the Willows (*Salix* spp.), some species of Campion (e.g. *Lychnis alba*), Dog's Mercury (*Mercurialis perennis*), and others. In such plants self pollination is clearly impossible.

A majority of species, however, have perfect flowers producing both stamens and ovaries. In these, attainment of maturity by the stamens before the stigmas or vice versa, or some structural device in the flower usually makes cross-pollination more likely to occur than self-pollination. Of special interest are those cases in which a species exists in two, sometimes in three forms differing in the relative positions of anthers and stigmas. In Primrose and other species of *Primula* there are two kinds of plants, one bearing flowers with long styles and anthers inserted some way down the corolla tube, the other having flowers with short styles and anthers inserted at the top of the tube. Pollen will adhere to different regions of the proboscis of an insect according to which of the two types of flowers is visited. The pollen carried away after a visit to a long-styled type of flower will be in a favourable position on the insect for bringing about pollination of the next short-styled flower visited; and vice versa. Cross-pollination between the two types is thus favoured although the possibility of pollination between two flowers of the same type, or even self-pollination within the same flower, is not excluded. In Wood Sorrel (*Oxalis Acetosella*) and Purple Loosestrife (*Lythrum Salicaria*) and other genera, three types of flower occur having three lengths of style and three corresponding anther positions.

By these and other means, cross-pollination within the species

is favoured; self-pollination, if less likely, is also usually possible except in unisexual species; pollination by a different species is possible in all.

Selective fertilization

There are two stages between pollination and fertilization; the pollen grain must first germinate on the stigma, after which the resulting pollen tube must grow through the style to reach the ovule. These stages provide opportunities for selection among the pollen grains reaching the stigma as to which may bring about fertilization; pollen from different species and from different plants of the same species may be present together but may differ greatly in their effectiveness in bringing about fertilization.

Germination of pollen grains can often be brought about by immersing them in a sugar solution, although those of different species may require different concentrations. Some grains fail to germinate whatever the concentration of the solution, but do so readily in a sugar solution of appropriate strength if a piece of stigma of the same species is added. Here then is one of the selective mechanisms; pollen grains falling on stigmas of the same species as themselves will find secretions favourable to their germination; those of some other species may find neither the concentration of the solution nor the special stimulatory substances secreted from the surface of the stigma suitable, so that these will germinate more slowly or not at all.

The growth of the pollen tube through the style takes place in the same way as does the growth of a parasitic fungus through the tissues of its host. And just as there is a limited range of species susceptible to attack by certain parasites, so a pollen tube, while able to grow in the stylar tissues of its own species, may fail to grow or grow more slowly in stylar tissues of flowers other than those of species to which the pollen belongs. If, therefore, several kinds of pollen reach the surface of the stigma simultaneously, that of the same species is favoured both in respect to germination and to subsequent growth of the pollen tube through the style; it will reach the egg-cell and bring about fertilization while

pollen tubes from the pollen of other species are still growing slowly through the style or have failed to germinate.

This kind of behaviour may also operate to favour cross-fertilization as compared with self-fertilization within the same species, being often combined with some structural device that favours cross-pollination. Thus the Primrose has two types of flower borne on different plants, an arrangement that favours cross-pollination (p. 163); but as observed and placed on record by Charles Darwin, if the flowers are artificially pollinated by hand so that pollen grains from a long-styled plant reach the stigma of another long-styled flower, or vice versa, this 'illegitimate' pollination is less effective in seed-production than the naturally occurring 'legitimate' pollination. So that should the pollination mechanism fail to prevent some degree of self-pollination, any pollen grains of the same type of flower are unlikely to effect fertilization of the egg-cell in competition with the more rapidly growing tubes produced by pollen grains of the alternative type of flower.

Although in some species self-pollination leads to lower seed production than does cross-pollination between different plants of the same species, in others it may be fully effective. There is a wide range in behaviour among species, some being completely self-sterile and yielding seed only when pollen is transferred from another plant, others showing varying degrees of self-sterility (see also p. 167).

Some interesting experiments have been carried out recently with a view to ascertaining the relative parts played by selective pollination and selective pollen-tube growth in a particular case. These concern two species of Antirrhinum, *A. majus* and *A. glutinosum*, which cross readily when pollinated artificially and give fully fertile hybrids. A large number of these two species were interplanted and left to bees to pollinate. Of the seeds collected from the *majus* plants, 0·6 per cent proved to be hybrids; of those collected from the *glutinosum* plants, 3 per cent were hybrids. In addition, a number of *glutinosum* flowers were hand pollinated with both *majus* and *glutinosum* pollen; these pollinations gave 41·6 per cent hybrid plants. That only 3 per cent hybrids were obtained from the *glutinosum* plants when pollination of the

mixed population was carried out naturally by bees, cannot therefore be accounted for by greater effectiveness in securing fertilization of *glutinosum* as compared with *majus* pollen when deposited on a *glutinosum* stigma. On the other hand, observation of the behaviour of the bees showed that any single insect confined its attentions to one species of plant for relatively long periods of time in spite of the intermixture of plants of the two species. In this case, therefore, it may be stated that the behaviour of the bees in discriminating between the two species is mainly responsible for the small number of hybrids produced, but that there is also some preferential encouragement to growth of pollen-tubes in styles of the same species, since hand pollinations with mixed pollen gave fewer hybrids than pure species in the progeny.[1]

Advantages of cross-fertilization

With so many complicated devices that favour cross-fertilization existing in nature it may well be asked what are the advantages and disadvantages of self- and cross-fertilization.

We have not the space to attempt to answer this question fully. One obvious advantage of cross-fertilization is that it results in a greater mixture of genetic factors, so giving opportunity for new combinations which may make the plant better adapted to its surroundings. The natural environment is under constant change and those plants that survive in the intense competition for place are those most supple in their power of adjustment to changing conditions.

An associated phenomenon of some practical importance is the increased vigour observable when naturally self-pollinated plants are cross-pollinated, a result referred to as *hybrid vigour*. In such cases the progeny grow more quickly and are larger than the parents. Hybrid vigour is expressed in maximum degree in the first generation cross, hence in plants raised from seed it becomes necessary to repeat the parental cross for each crop if

[1] Mather, K. 'Breeding systems and genetic isolation.' John Innes Hort. Inst. *Ann. Rep.* *36*, 15, 1945.

maximum vigour in plants raised from seed is required. This is a relatively easy matter if the sexes are borne on different plants, otherwise artificial pollination by hand must be resorted to, an operation which may prove too laborious to be profitable commercially. On the other hand, in plants that can be propagated vegetatively, the vigour of the first generation hybrid can be maintained indefinitely by propagation from cuttings, grafting, etc. Hybrid vigour has been successfully exploited on a commercial basis in maize, tomato, potato and cucumber, of which seeds of first-generation crosses giving maximum yield can now be purchased through seed merchants.

While the primary result of successful germination of the pollen grains and development of pollen tubes is fertilization of the egg-cell and the production of fertile seeds it is not the only one; secondary effects are produced on other parts of the flower leading to the formation of fruits which are often of more immediate interest to man than the seeds. The edible part of fruits such as apple, pear, quince or strawberry consist of the swollen flower stalk or receptacle, that of cherries and plums of the swollen carpel walls, that of mulberries of swollen petals and other floral parts; all these fruits normally require successful pollination and fertilization for their production.

Incompatibility

An important aspect of practical fruit growing is that many commonly cultivated varieties of fruit trees are self-sterile or better described as 'self-incompatible'. All varieties of sweet cherries, for example, are self-incompatible and fall into nine intra-sterile and inter-fertile groups.

Similar behaviour occurs in plums and apples, although partially self-compatible varieties are known among both these kinds of fruit trees. Such facts are of critical importance in the planting of an orchard. Should it be desired to grow the variety of cherry 'Bedford Prolific' for instance, it must not be planted alone because little fruit will set, the variety being self-incompatible; it is not even helpful to interplant with varieties such as

'Early Rivers' or 'Knight's Early Black' for with these 'Bedford Prolific' is also incompatible; it is necessary to interplant with some variety with which 'Bedford Prolific' is compatible and of these there is a large choice, e.g. 'Waterloo', 'Turkey Heart', 'Elton', etc. If satisfactory fruit crops are to be ensured it is

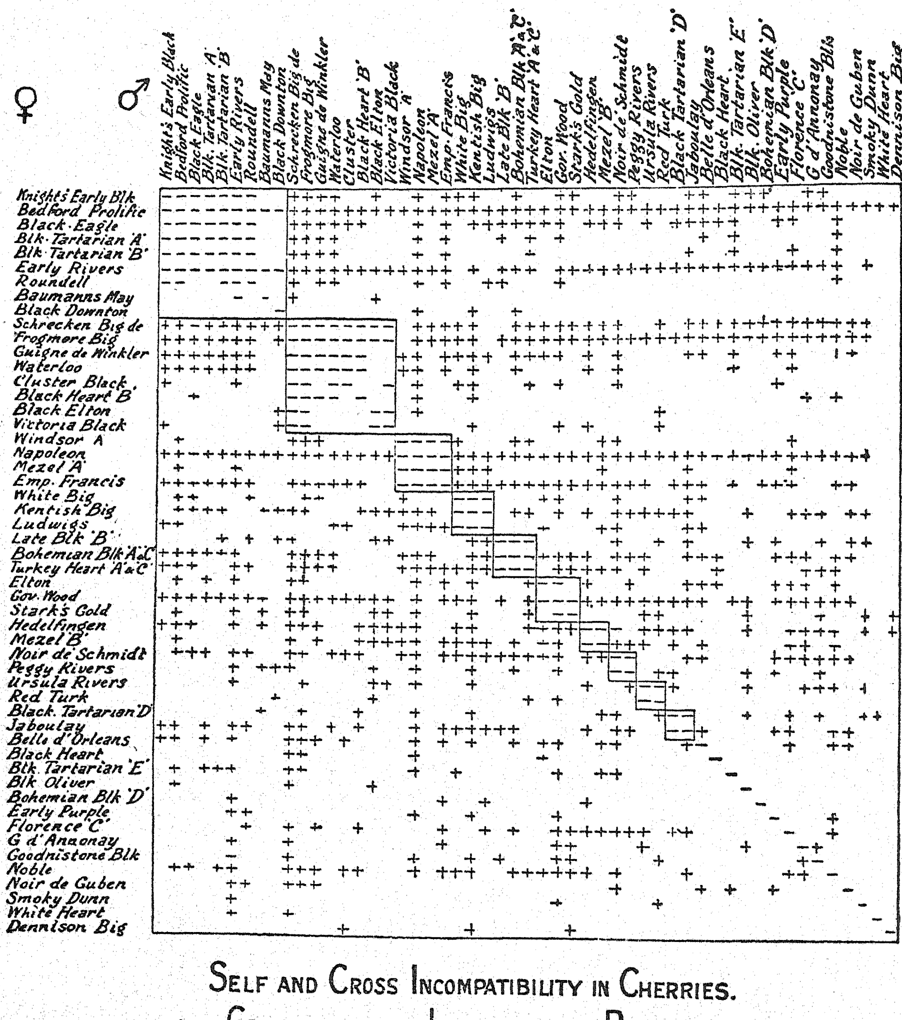

FIGURE 32

Compatible and incompatible varieties of cherry.

obviously wise to consult the data now available as to varieties that are compatible and incompatible with those it is desired to grow, and to take into account all the facts now known concerning these matters (fig. 32).

Sterility of this kind is called incompatibility because the pollen and ovules are normal and functional under appropriate conditions; failure to set seed and fruit is not due to any defect in the reproductive organs or to abnormality in the reproduction process. It appears to be due to the plants carrying genes or hereditary factors (p. 173) which may be designated S_1, S_2, etc., which operate so that a pollen grain carrying S_1 cannot grow or grows sluggishly down the style of a plant also carrying S_1, but suffers no such inhibition if growing in the style of a plant carrying S_2, S_3, etc. (fig. 33). This means that no

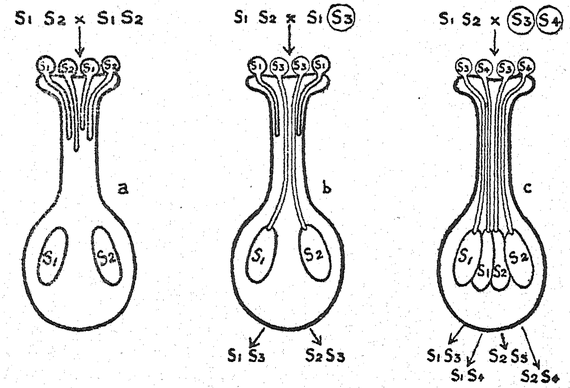

FIGURE 33

Diagrams of pollen tube growth following compatible and incompatible pollinations. *a* shows the restricted growth of pollen tubes carrying S_1 or S_2 in a style carrying S_1 and S_2, the condition obtaining in a self-pollinated plant. *b* shows the result of pollinating a plant carrying S_1 and S_2 with pollen grains carrying either S_1 or S_3; only those with S_3 are effective. *c* shows the result of pollinating a plant carrying S_1 and S_2 with pollen grains carrying S_3 or S_4, both of which are effective.

plant carrying 'incompatibility genes' can set seed with its own pollen if the incompatibility is complete. A sample of the kind of data available for cherry is given in figure 32.

Seedless fruits

Since the biological function performed by the fruit is to protect the seeds or help in their distribution, there would appear to be no purpose served in producing a fruit that did not contain seeds. Nevertheless, there are a number of plants in which the stimulus following pollination leads to production of fruits but in which fertilization of the egg-cell and seed formation does not occur.

This is true, for example, in seedless varieties of oranges, seedless grapes such as sultanas and most of the cultivated varieties of bananas and cucumbers. In these, although development of the pollen grains does not succeed in bringing about fertilization of the egg-cell, it provides the stimulus necessary for fruit formation. This behaviour suggests that the pollen grains contain some chemical substance the presence of which is responsible for initiating the special kind of growth that leads to the formation of the fruit. It has been now discovered that unpollinated flowers of tomato or potato, or flowers with the anthers removed, develop fruits if the flowers are sprayed with crude extracts of whole flowers or with pollen extracts. Many growth-controlling substances, including indole-acetic acid (heteroauxin), have a similar effect and are now employed for spraying tomatoes grown on a commercial scale, especially at the beginning and end of the season when fruits may set badly under natural conditions.[1] A further practical application of this discovery is the spraying of fruit trees, blossoms of which have been so damaged by frost as to set little fruit. Some varieties of apple have been found to respond very favourably to such treatment, a good crop being obtained from the treated trees in contrast to almost complete failure in untreated trees.

Yet another direction in which growth substances have found practical application depends on their ability to delay formation of the abscission layer to which the shedding of leaves and other organs is due. Some varieties of apple, for example, are liable

[1] Swarbrick, T. 'Parthenocarpic production of Tomato fruits.' *Nature, 156*, 300, 1945.

to premature development of the abscission layer responsible for the normal shedding of the ripe fruit. This behaviour, known as 'pre-harvest drop', may appreciably reduce the amount of marketable fruit obtained; development of the abscission layer may often be delayed by use of appropriate growth substances and losses from pre-harvest drop be substantially lessened. Naphthalene-acetic acid appears to be one of the most effective substances among the many that have been used and is a frequent constituent of the various proprietary products that have been put on the market to control fruit drop.

The dropping of cut flowers when due to the formation of an abscission layer may often be delayed by similar treatment.[1]

Chromosomes—genes—mitosis

We come now to some important aspects of sexual reproduction related to the structure and behaviour of the nucleus, unfortunately a highly complex and difficult subject. Some consideration of nuclear behaviour during the process of cell and nuclear division cannot be avoided for an understanding of the matters dealt with in the remainder of this chapter; by limiting ourselves to those facts essential for an appreciation of the subjects to be discussed we can evade most of the difficulties complete study of nuclear behaviour entails.

The bodies of plants and animals are composed of fundamental units called *cells*. Besides various non-living components, such as the cell wall, starch grains and various substances in solution, the cell contains the essential living substance *protoplasm*. The most important part of the protoplasm from our present point of view is a specialized structure called the *nucleus*. This is distinguished by greater density and by greater capacity for absorbing certain dyes. Typically, every cell is provided with one nucleus. The instances in which a cell appears to possess

[1] Vyvyan, M. C. 'Fruit fall and its control by synthetic growth substances.' *Imp. Bur. of Hort. and Plantation Crops Tech. Communication No. 18.* 1946. (Imp. Agric. Bur., Penglais, Aberystwyth.)

more than one nucleus may be regarded as cases in which the limits between several cells, each with one nucleus, are not clearly defined or demarcated by cell walls. No cell appears to be able to carry out vital functions for long in the absence of a nucleus; the rare exceptions, such as the red blood corpuscles of mammals, are all cells with a transitory existence and are incapable of reproducing their kind.

The nucleus contains a number of thread-like or rod-like bodies called *chromosomes*, clearly defined during the process of nuclear division but at other times diffused throughout the nucleus and difficult to distinguish one from another. The number of chromosomes possessed by the nucleus is definite and characteristic for every species or variety of organism; for example, the nuclei of Sweet Pea (*Lathyrus odoratus*) and the Garden Pea (*Pisum sativum*) possess 14, Tiger Lily (*Lilium tigridum*) 24, Oriental Poppy (*Papaver orientale*) 42, while those Man have 48; both higher and lower numbers are met with, but the majority of plants and animals fall within the range indicated. A further point of importance is that individual chromosomes frequently differ sufficiently from one another in size and other ways to make it possible to recognize particular chromosomes.

Vegetative growth is brought about by multiplication of cells; each cell increases in size and then divides to form two daughter cells. Cell division is preceded by division of the nucleus during which the chromosomes pass through a regular series of changes. To begin with they gradually lose the indefiniteness they had before the nucleus began to divide, become sharply defined, and arrange themselves in one plane. Having attained this position, each undergoes longitudinal fission and the members of each of the pairs so formed separate from one another to constitute two groups at opposite ends of the cell, each containing the same number of chromosomes as the original nucleus. The definiteness of the individual chromosomes in each of the groups becomes progressively less obvious and the condition of the 'resting' nucleus is finally reassumed. Meanwhile a new cell wall is usually laid down between the two new nuclei, dividing the original cell in two exactly similar daughter cells (fig. 34).

Other structures may appear and disappear during this process; these for the present purpose we can ignore.

The elaborate character of this process is required in order to ensure not only that the newly formed nuclei shall contain the same number of chromosomes as the original nucleus, but that each individual chromosome shall be divided into two exactly similar parts. This is necessitated by the fact that the *genes* or bearers of the hereditary traits of any plant or animal are arranged in a single row along the chromosomes, so that each chromosome must divide along its entire length if the two portions are to contain the same genes similarly arranged.

Establishment of the fact that the hereditary genes are arranged in a single row on the chromosomes and determination of not only which chromosomes carry which genes but the relative positions of the different genes on the chromosomes represents a deductive achievement in the biological field comparable with that of determining the spacial arrangement of the atoms forming a chemical compound in the field of chemistry. In both genes and atoms we are dealing with entities too small to be directly visible, whose very existence is based on deduction, and yet whose relative position in space we can define with considerable accuracy. As a result of breeding experiments combined with parallel cytological investigation it has been possible to construct chromosome maps for many plant and animal species, indicating the genes carried by each chromosome and the relative positions of these along the chromosomes. From such maps it is possible to forecast the qualitative and numerical results that will follow from any cross in which the genetic make-up of the parents is known.

This elaborate process of nuclear division, called *mitosis*, ensures that at each vegetative division a nucleus gives rise two nuclei identical to itself and containing identical hereditary potentialities.

Meiosis—fertilization

While mitosis serves to maintain nuclear stability during vegetative growth, a new situation arises with sexual reproduction.

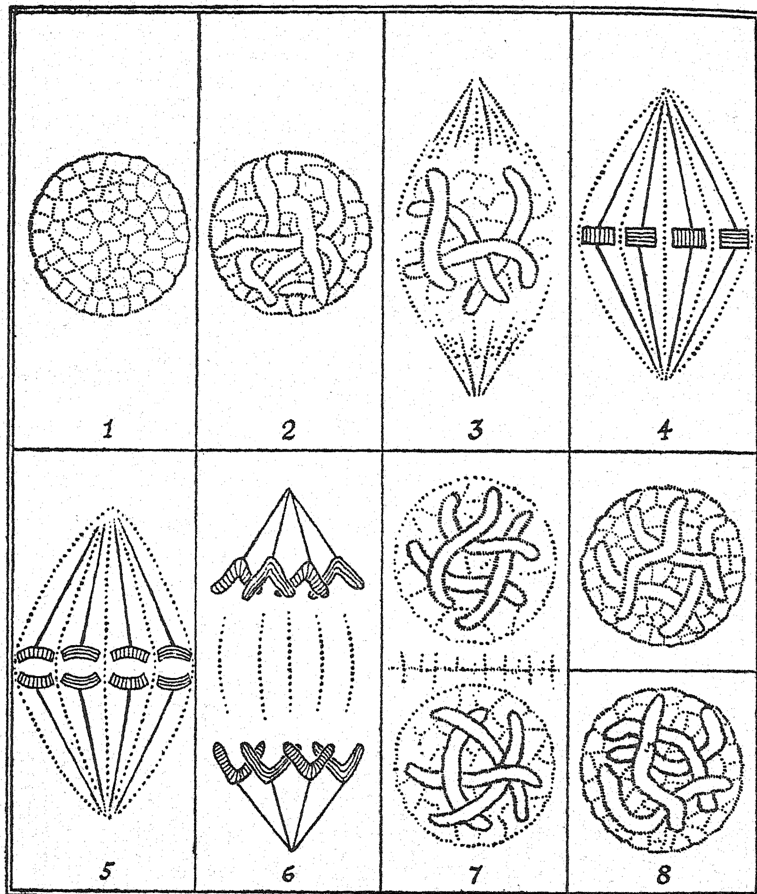

FIGURE 34

Stages in nuclear division or *mitosis*: greatly simplified and diagrammatic.

(1) 'Resting' nucleus surrounded by nuclear membrane. (2) Resolution of nuclear network into recognizable chromosomes. (3) Chromosomes clearly defined, disappearance of nuclear membrane and organization of spindle fibres. (4) Arrangement of chromosomes in a median plane; a 'traction fibre' attached to either side of each chromosome; 'supporting fibres' running from pole to pole unattached to the chromosomes. (5) Each chromosome split into equal halves. (6) The two groups of chromosomes separating. (7) and (8) the condition of the resting nucleus as shown in stage (1) gradually resumed with reappearance of the nuclear membrane.

In sexual reproduction, two specialized sex cells, or gametes, fuse to produce a cell from which, as a result of repeated mitotic divisions, the new individual arises; this individual in turn produces gametes whose fusion leads to the next sexually produced generation and so on. The two gametes undergoing fusion may show little difference from one another as in some of the lower plants, but in Flowering Plants they differ and can be distinguished as male and female, the former produced by the pollen grains within the anthers, the latter by the embryo sac within the ovules. The process of fusion in this case is called *fertilization.*

If we examine the nuclei within the pollen grains or that of the egg-cell within the embryo sac in, say, Maize, we find they contain ten chromosomes, all recognizably different from one another and constituting the complete 'set' of chromosomes characteristic of Maize. When a male and female gamete unite, that is, when the egg-cell is fertilized, there is a fusion between two nuclei each with a set of ten chromosomes. The fertilized egg-cell and all the cells of the plant developing from it consequently have nuclei with two sets or twenty chromosomes, two sets of ten each. This plant in due course produces its own gametes; these are found to possess nuclei with only one set of chromosomes. There is thus a regular alternation between two nuclear conditions, that in which there is a single set of ten chromosomes and that in which there is a double set amounting to twenty chromosomes.

Doubling in the number of chromosomes is clearly accounted

FIGURE 34—*continued*

The supporting fibres are most persistent in the region in which the new cell-wall appears.

The above figures represent nuclear division during vegetative growth of a sexually produced individual the nuclei of which usually contain two chromosome sets, one derived from each parent, each kind of chromosome thus being represented twice. This is indicated in figures (4), (5) and (6) by the different directions of lines of shading on the chromosomes. For simplicity, the number of different kinds of chromosomes constituting a set is shown as two; in most plants it is greater than this, numbers between 7 and 12 being common, although numbers greatly in excess of these are not unusual.

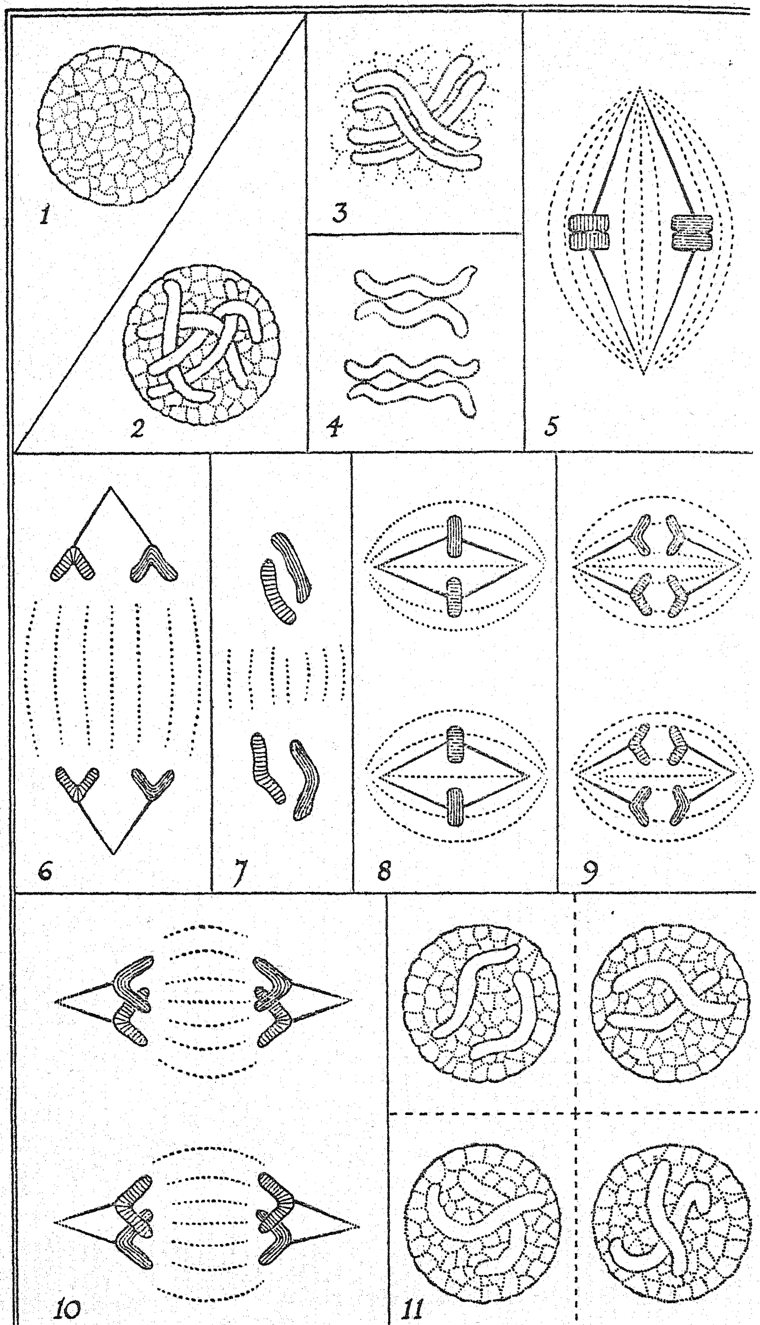

FIGURE 35

for by fusion of the two nuclei at fertilization; return to a condition in which only a single set is present is due to a special reduction process that comes into operation before gamete formation. This reduction process occurs during a phase in the life history known as *meiosis* involving two closely associated nuclear divisions. During these two divisions the chromosomes go through a highly intricate series of changes and interchanges upon which depend the distribution of the hereditary characters of the two parents among the offspring.

One type of such distribution was discovered by Mendel from breeding experiments and is embodied in the so-called Laws of Mendelian Inheritance, published in 1865. That the behaviour of the chromosomes provided the mechanism for bringing about

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FIGURE 35

Stages in *meiosis*, the nuclear phase that precedes the formation of sex cells or gametes, consisting of two 'divisions', and resulting in a halving of the number of chromosomes present: highly simplified, and diagrammatic.

(1) 'Resting' nucleus surrounded by nuclear membrane. (2) Resolution of nuclear network into *four* recognizable chromosomes (the *diploid* number). (3) Chromosomes clearly defined and associated in pairs of similar kind (*homologous*); disappearance of nuclear membrane. (4) The members of each pair develop repulsion towards each other, but cannot separate completely since they are held together at certain places by the intercrossing of internal threads (not shown in the diagram). (5) Final shortening and condensation of the chromosomes, their arrangement in a median plane and the development of spindle fibres. (6) Previously paired chromosomes separate from one another. (7) The chromosomes of each group arrange themselves in planes perpendicular to that previously occupied. (8) Development of spindle fibres. (9) Each chromosome becomes split into two equal halves. (10) Formation of four groups of chromosomes. (11) The 'resting' condition, as shown in stage (1), is gradually resumed, each nucleus containing *two* chromosomes (the *haploid* number).

The final result of this process is to give four nuclei in place of the original one, each of the four possessing half the number of chromosomes as the original nucleus. As indicated in stages (5) to (10) the chromosomes that associate in pairs are similar in kind or *homologous*; so that if the original nucleus possessed two complete sets of chromosomes, the resulting four nuclei each contain a single set.

Note. The actual behaviour is much more complex than indicated in these diagrams; for instance, interchange of equivalent portions of the homologous chromosomes shown as paired in stage (5) takes place before the separation shown in stage (6). This has important effects on the distribution among the sex cells of the hereditary factors or genes carried on the parts undergoing exchange.

this distribution did not become apparent until half a century later.

The first division of meiosis differs from an ordinary vegetative division or mitosis in that instead of behaving independently and arranging themselves in one plane prior to longitudinal fission, the chromosomes associate in pairs; it is these paired chromosomes that arrange themselves in a median plane. The effect of the remaining stages of this division and of the one immediately following is to separate the members of these pairs into two groups from which the new nuclei are constituted (fig. 35). Actually the process is far more complicated than this, because after the pairing of similar chromosomes and before their separation, interchanges may occur between equivalent portions of the members of each pair, resulting in the interchange of the hereditary genes carried by these portions.

The chromosomes that pair are always of the same kind, so that if we call the ten chromosomes of the set in Maize I, II, III, to X, then I pairs with I, II with II, and so on. Consequently the process of meiosis leads not only to the production of nuclei containing ten instead of twenty chromosomes, but the ten chromosomes are always a complete set, every type of chromosome from I to X being represented once and once only. An important part of this process is the preliminary sorting out and association of *similar* chromosomes in pairs. If the pairing took place in any other way, each of the new nuclei would possess ten chromosomes but these would not form a complete set, one or more types being represented twice and others absent.

We are now in a position to proceed with our discussion of sexual phenomena in plants.

Mutations—polyploids

One of the anomalies that appear in large-scale breeding is the occurrence from time to time of plants having some entirely new and unexpected character not to be explained as due to some unusual combination of the genes known to be present. These unexpected individuals arising suddenly and sporadically

in a population may be attributed in general to some constitutional change in a chromosome or part of a chromosome or to some failure of the sorting mechanism at nuclear division; they are called *mutations*. Among the various kinds of mutations that occasionally appear are those in which the flowers and other parts of the plant are conspicuously larger and more massive than usual.

One of the first of these giant forms to be fully investigated was that appearing in the Chinese Primula (*Primula sinensis*). The giant form was found to be fully fertile when pollinated with its own pollen or with pollen from other giant plants, giving giant plants like itself. If pollinated with pollen from the normal form or if the reciprocal cross were made, the seed obtained by such means produced plants that showed a high degree of sterility.

Study of the nuclei and nuclear behaviour in the two varieties and in the hybrid between them provided an explanation of these observations.

The normal form of *P. sinensis* possesses twenty-four chromosomes (two sets of twelve) and gives rise to gametes with twelve chromosomes (one set), so that the fertilized egg-cell from which the next generation arises has again twenty-four chromosomes. The giant form has forty-eight chromosomes (four sets of twelve) giving rise to gametes containing twenty-four chromosomes (two sets). In view of the number of chromosome sets present, the former is said to be a *diploid*, the latter a *tetraploid* plant.

In the hybrid between diploid and tetraploid plants, the gamete from the former contributes one set of chromosomes, that from the latter two sets, making three sets or thirty-six chromosomes in all after fertilization. The plants arising from such a fertilized egg-cell are therefore known as *triploids*. The fertilized egg-cell containing three sets of chromosomes grows without difficulty into a triploid plant, because during vegetative growth nuclear division takes place by mitosis in which each chromosome behaves as an independent unit. When, however, the time arrives for this triploid plant to form gametes and the preliminary process of meiosis is entered upon, difficulties arise. The first stage of meiosis consists in the pairing of like

chromosomes, the members of each pair being subsequently segregated into the new gametes. But in a triploid, each type of chromosome is represented three times, so that it is impossible for all to form pairs. What frequently happens is that three similar chromosomes become associated in a group in which equivalent parts of different chromosomes pair (fig. 36). Instead of a precise separation of *whole* chromosomes as there should be in the subsequent stages of meiosis, odd fragments of chromosomes will be contributed haphazard to the resultant nuclei. Not possessing a complete and balanced set of chromosomes, the pollen grains and egg-cells cannot function normally, i.e. the plant will be sterile.

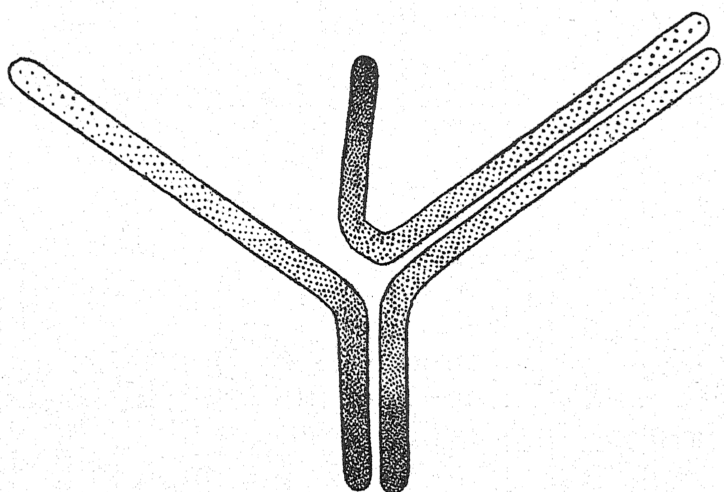

FIGURE 36

In a variety with three sets of chromosomes (triploid), association of similar (homologous) chromosomes during early meiosis leads to aggregations like that shown in which pairing of homologous *regions* of the chromosomes occurs. Distribution of whole chromosomes to the gametes in the subsequent stages of meiosis is unlikely to result from such complexes; hence the high degree of sterility of triploid races and of other polyploids with an uneven number of chromosome sets in the nuclei.

The situation is very different in the case of the plant derived from crossing together two tetraploid plants. This possesses four

chromosome sets, two derived from each parent. At meiosis, as in the diploid, each kind of chromosome can find a similar or 'homologous' partner with which to pair; separation and distribution of whole chromosomes can take place normally; as a consequence the plant is usually fertile, producing functional pollen grains and egg-cells, with development of fertile seed after fertilization.

Plants having more than the normal two sets of chromosomes are given the general name of *polyploids*; besides triploids and tetraploids they include plants with still larger numbers of chromosome sets, such as *hexaploids*, *decaploids* and even higher numbers. From the observed behaviour of the chromosomes in triploid and tetraploid plants during meiosis it follows that plants with an uneven number of chromosome sets will be sterile and that only those with an even number of sets will be fertile, since only in the latter can every chromosome find a partner like itself with which to associate and thus ensure distribution of complete sets of whole chromosomes to the gametes.

In general, tetraploid plants are notably larger than those of the normal diploid stock; the possession of larger flowers in particular gives them a special value to the commercial grower who is apt to regard bigger as synonymous with better. But whilst increase in number of chromosomes often finds expression in increased size of flowers and other organs this is not invariably the case—it may even lead to reduction in size, especially in forms higher in the series than tetraploid. In other words; the number of chromosome sets associated with maximum vigour of growth depends upon the species.

In the polyploid series, members with uneven numbers are, in general, of less interest to growers than those with even numbers owing to the invariable sterility of the former, although this rule does not apply to plants readily propagated by vegetative means. Such well-known varieties of apple as 'Bramley's Seedling', 'Ribston Pippin' and 'Blenheim Orange'; many outstanding varieties of hyacinth such as 'King of the Blues', 'Queen of the Pinks'; some of the highly decorative Japanese cherries and other valued plants of our gardens, are all triploid in respect of their chromosome sets.

The demand of the horticulturist is not only for 'giant' tetraploid plants, but also for these in as great a range of forms and flower colours as in diploid plants. Transfer of characters from diploid to tetraploid forms by breeding is a long and tedious process; it would be an enormous advantage if diploid plants of the required colour or form could be induced to produce tetraploid mutations. Not only *Primula sinensis*, but many other plants in which the tetraploid form is more vigorous would be welcomed by the horticulturist and others interested in the growing of plants. It has even been suggested that the forester might benefit from more vigorously growing tetraploid races of trees, although the benefit here is more problematical as it does not follow that more rapidly growing trees would produce as good quality timber. On the other hand, enormous quantities of wood are used annually in the manufacture of paper and in other industries where the qualities called for are very different from those required when it is used as a structural material. In Sweden, for example, the match industry is exploiting a very rapidly growing variety of Poplar which is almost certainly a tetraploid.

In general, then, there is a strong demand for tetraploid varieties in many kinds of plants; any methods by which these can be produced artificially without waiting for the rare and uncertain appearance of natural mutations would be of considerable interest.

Artificial production of polyploids

Several treatments have been discovered for encouraging the appearance of polyploid varieties. The simplest of these is by wounding the tissues of vigorously growing plants. If the stems of tomatoes or potatoes are cut back, the wound is overgrown by a tissue called *callus* from which numerous buds arise subsequently. In the plants mentioned an appreciable percentage (7 per cent or more) of the new shoots have tetraploid nuclei or possess regions more or less extensive in which this occurs, the latter being in fact nuclear chimaeras (p. 43).

Another method found successful in some cases is exposure to high temperatures. Among other abnormalities tetraploid plants result when seedlings of maize are exposed to temperatures of 38° to 45° C. (100° to 112° F.) for several hours at intervals of four hours. In view of these results it has been suggested that intermittent high temperature in nature may have played a part in the spontaneous appearance of polyploids.[1]

Exposure to X-rays and the emanations from radio-active substances also brings about nuclear abnormalities, among them a polyploid condition.

Many chemical substances induce the formation of tetraploid nuclei; such simple substances as copper nitrate, lead nitrate and other inorganic salt solutions applied in high dilution have been found to affect onion roots in this way.[2] Perhaps most remarkable of the chemical substances known to induce polyploidy in plants is colchicine, widely exploited in recent times owing to the number of plant species affected by it.[3] [4] [5] Colchicine is extracted from the tissues of the Meadow Saffron (*Colchicum autumnale*). It is toxic to plant tissues when applied in high concentration but in sub-lethal doses it brings about the production of tetraploid nuclei in dividing cells. Little doubt exists as to its mode of action; namely, inhibition of the mechanism responsible for the separation of the two daughter chromosomes formed by equational division of each chromosome during mitosis without interference with the division process. As a result, instead of the two groups of new chromosomes separating to form two new nuclei with the usual number of chromosomes as in normal mitosis, they remain in close association and are ultimately incorporated to form a single nucleus having double the normal number of chromosomes. Not the least remarkable feature about

[1] Randolph, L. F. *Some effects of high temperature on polyploidy and other variations in maize.* Proc. Nat. Acad. Sci., U.S.A., *18*, 222, 1932.

[2] Levan, A. 'Cytological reactions induced by inorganic salt solutions.' *Nature*, *156*, 751, 1945.

[3] Blakeslee, A. F. and Avery, A. G. 'Methods of inducing doubling of chromosomes in plants.' *Jour. of Heredity*, *28*, 392, 1937.

[4] Levan, A. 'The effect of colchicine on root mitoses in *Allium*.' *Hereditas*, *24*, 471, 1938.

[5] Levan, A. 'The effect of colchicine on meiosis in *Allium*.' *Hereditas*, *25*, 9, 1939.

colchicine is that while producing remarkable effects on the dividing cells of many plants, it is apparently without action of any kind on *Colchicum*, the plant species forming it.

Colchicine is used in a number of different ways; it can be applied in concentrations up to 0·4 per cent as a watery solution in which the tissue to be treated is immersed or with which it is sprayed; or it may be mixed with lanolin to form a paste with which the part of the plant under experiment is smeared. These methods have been used successfully on seeds, stem tips and root tips.

Increase in number of chromosomes may be induced also by strong solutions of growth-promoting substances such as heteroauxin or indole-acetic acid (p. 72). At naturally occurring concentrations, heteroauxin brings about cell elongation without interfering with normal mitoses at the stem tip; at high concentrations an additional effect is produced—enlargement and divisions of mature cells in the cortex appearing externally as swellings. Twice the normal number of chromosomes make their appearance in the early stages of nuclear division in these cortical cells, so that doubling must have occurred during the *resting* stage of the nucleus. The mechanism leading to the formation of tetraploid nuclei must be different in this case from that operating under treatments with colchicine.[1]

Polyploids and the origin of new species

From the foregoing it is clear that a number of methods are now available for producing tetraploid and other polyploid forms artificially with relative ease instead of relying on their infrequent and irregular origin as natural mutations. Which of the methods will be most effective in any given case can be determined only by trial. Apart from economic advantages associated with the ready production of tetraploids, the conditions that lead to their appearance acquire increased interest with fuller realization of their significance in the origin of new

[1] Levan, A. 'Cytological phenomena connected with the root swelling caused by growth substances.' *Hereditas, 25*, 87, 1939.

species. The importance of polyploidy in this connection may be illustrated by reference to the history of the origin of *Primula kewensis*, a hybrid species of Primula.

Primula verticillata and *P. floribunda* are two well-known yellow-flowered species of Primula often cultivated in greenhouses in this country. Both have eighteen chromosomes consisting of two sets of nine which for convenience may be designated V1, V2, V3, to V9 and F1, F2, F3, to F9 respectively. If flowers of *P. verticillata* are pollinated by flowers of *P. floribunda*, seed is obtained which germinates to give a hybrid plant, *P. Kewensis* which is completely sterile. The reason for sterility becomes evident if we consider what happens in regard to the chromosomes of the hybrid at meiosis. When *P. verticillata* is fertilized by *P. floribunda*, a gamete containing a set of V chromosomes unites with one containing a set of F chromosomes. The nuclei in the hybrid plant developed from the fertilized egg-cell contain therefore eighteen chromosomes; namely a set each of nine V and nine F chromosomes. When the hybrid enters upon meiosis as a prelude to the formation of sex cells or gametes, no chromosome is able to find a partner with which to pair, since V1, for example, is not homologous with F1 nor with any other chromosome present. The mechanism for sorting out a complete set of chromosomes for distribution to each gamete consequently breaks down, as a result of which neither good pollen nor viable egg-cells are formed and the plants are sterile.

Although this hybrid plant with its eighteen chromosomes is sterile, producing no seed, it grows quite well since vegetative growth involves only mitotic nuclear divisions in which each chromosome behaves as an individual unit; it is perennial and with care can be kept in cultivation indefinitely by vegetative propagation.

On several occasions this hybrid has produced spontaneously, after being some time in cultivation, a branch bearing viable seed. The seedlings derived from this are larger than the parent sterile hybrids and bear larger flowers fully fertile with one another although not with either of the original species parents. Examination of the dividing nuclei of these plants or of the fertile branch on the sterile hybrid from which they were

derived, show that they contain thirty-six instead of eighteen chromosomes; the diploid sterile species hybrid has evidently produced a tetraploid shoot and with doubling of the chromosome number has become fertile. In the tetraploid form, in contrast to the diploid, every chromosome has a homologue with which it can pair at meiosis since there are two V1s, two F1s, two V2s, two F2s, and so on; the mechanism whereby a complete set of chromosomes is sorted out and distributed to the gametes can therefore function.

Now had this tetraploid plant of *P. kewensis* been met with in nature it would have been undoubtedly ranked as a true species; it shows characteristics sufficiently distinct to separate it from either *P. verticillata* or *P. floribunda* and to give it specific rank; moreover, if hybrids are formed with either of these species they will be triploid in respect to their nuclei and therefore sterile.

A parallel case to *Primula kewensis* is that of the grass named *Spartina Townsendii*, the history of whose origin is as follows. The genus *Spartina* is found chiefly on the Atlantic coast of America; in Europe there is one species, *S. stricta*, indigenous on the south and east coasts of England where it grows in the shallow brackish waters of estuaries; it is not a particularly vigorously growing plant.

In 1836 a colony of an American species, *S. alterniflora*, was recorded in Hampshire at the mouth of the River Itchen. In 1870 a third species, hitherto unknown, appeared at Hythe on Southampton Water and was named *S. Townsendii*. This grew with great vigour and by 1899 colonies of the plant had invaded Poole Harbour; so vigorous has been its growth in these two places that it has become a serious menace to shipping by causing the silting up of large areas of previously navigable waters. Meanwhile the plant has been establishing itself in one after another of the estuaries in the south-east of England, subjugating the native *S. stricta* wherever in competition with it. In 1906 *S. Townsendii* was recorded from the Normandy coast where it is also causing anxiety by invading and monopolizing estuarine waters.

Examination of the nuclei shows that *S. stricta* possesses fifty-six and *S. alterniflora* seventy chromosomes, their gametes con-

taining twenty-eight and thirty-five chromosomes respectively. A hybrid between these species would thus possess twenty-eight plus thirty-five, equalling sixty-three chromosomes, and a tetraploid form of the species hybrid would have 126 chromosomes; this is the number occurring in *S. Townsendii.*

These numbers enable us to reconstruct the historical events that led to the origin of *S. Townsendii* along the following lines.

S. Townsendii made its first appearance in the neighbourhood of ports used by shipping from America in the vicinity of which *S. stricta* was growing. It is highly likely that *S. alterniflora* was accidentally introduced from the east coast of America by one of these ships and having established itself formed a hybrid with the native *S. stricta*. As with *Primula kewensis*, the species hybrid was sterile but was able to maintain itself without difficulty owing to its effective vegetative propagation, in this case by means of a creeping rootstock. Eventually a tetraploid shoot arose which produced fertile seed, the seedlings derived from which would show all the vigour associated with hybrids and tetraploids and would constitute *S. Townsendii*. Both in respect to the historical record and from the chromosome conditions in the three plants the evidence could hardly be more complete that *S. Townsendii* is a strictly parallel case to that of *Primula kewensis*.[1]

There are a number of other plants of which one may say with a degree of probability that amounts to certainty that they are species hybrids in polyploid condition. Thus, *Aesculus carnea*, the Pink Horse Chestnut, is now recognized as being a tetraploid hybrid between *Ae. Hippocastanum*, the White Horse Chestnut, and *Ae. pavia*, the Red Buckeye. This view is supported by comparative chromosome studies as well as by comparison of morphological features. Forty chromosomes occur in both of the two last named species, the gametes containing twenty chromosomes. The nuclei of the species hybrid should thus contain forty chromosomes, while the tetraploid form of this species hybrid should possess eighty chromosomes; this is, in fact, the nuclear condition found in *Ae. carnea*.

As a further example may be mentioned the Common Hemp

[1] Huskins, C. L. 'The origin of *Spartina Townsendii*.' *Genetica*, *12*, 531, 1931.

Nettle, *Galeopsis Tetrahit*. *G. pubescens* (sixteen chromosomes) artificially crossed with *G. speciosa* (sixteen chromosomes) has given a fertile hybrid with thirty-two chromosomes; this is indistinguishable from the naturally occurring *G. Tetrahit*, which also has thirty-two chromosomes. There can be no doubt that *G. Tetrahit* which features in most floras as a British species is a tetraploid hybrid between the first two species mentioned.

Facts such as these amount to proof that one way by which new species arise in nature is by formation of a species hybrid followed by doubling in the number of chromosomes. Such plants will be fertile among themselves, but when crossed with other species, including the parents, will either be incompatible and produce no seed or beget sterile hybrid offspring—one of the criteria of a 'species'. Although the origin of *Galeopsis Tetrahit* as it occurs in nature from a cross between *G. pubescens* and *G. speciosa* may be regarded as certain, it remains unknown when and where this event took place; it is more than likely, indeed, that it may have occurred more than once. The existence of data as to both where and when *Spartina Townsendii* first made its appearance is one of the features of special interest in this plant.

The relations shown between the chromosome numbers of species included within a genus is often suggestive of a polyploid series. In many genera the species have chromosome numbers that are simple multiples of some basic number. Thus, in the Wheats (*Triticum* spp.) the basic number is seven and species with fourteen, twenty-eight and forty-two chromosomes are known; in *Chrysanthemum* the basic number is nine and species with eighteen, thirty-six, fifty-four, seventy-two and ninety chromosomes occur; in Poppy (*Papaver*) there appear to be two basic numbers, seven and eleven, corresponding with which species are on record with fourteen, twenty-eight, forty-two, seventy, twenty-two and forty-four chromosomes. In such cases it is tempting to suggest that species forming the higher members of the chromosome series have arisen by successive steps involving the production of polyploids in combination with inter-crossing between species. Such an hypothesis would imply that, in general, species with lower multiples of the basic num-

ber of chromosomes are of longer standing in this evolutionary sense than those with larger chromosome numbers. It must be borne in mind, of course, that polyploidy alone does not constitute a specific difference. Increase in the number of sets of chromosomes possessed by a species leads to the production of polyploid *varieties* of that species; the production of a new species requires that some of the additional sets in the polyploid plant shall be different from those borne by the seed parent, a result that follows from species hybridization.[1]

These facts have the further interest that they suggest means of producing new species artificially. For it is not uncommon for species when crossed together to give viable seed, but the resulting plants are, for the reasons discussed, sterile. In nature, the species hybrid, being sterile, will leave no offspring and will not persist beyond its own life span unless it happens to possess an effective means of vegetative propagation. Even if this exists, it may not be able to compete successfully with members of the natural vegetation in nature although it may possess features of horticultural or agricultural value and be capable of survival by continued vegetative growth under the protected conditions of artificial cultivation. In all probability species hybrids are being continually produced in considerable numbers under natural conditions, but survive longer than one generation only on the rare occasions when a tetraploid mutation arises early in their existence. The possession of artificial means such as treatment with colchicine for inducing a tetraploid constitution in such plants and so making them capable of producing fertile seedlings, places in the hands of the plant breeder a powerful instrument for producing new forms of plants with all the characteristics of true species. It must be remembered also that the range of species that can be hybridized has been enormously extended by the discovery of methods for controlling the times at which different species produce their flowers, whereby those normally flowering at widely different times of year can be

[1] Polyploids resulting from multiplication of the existing chromosome set beyond two are known as *autopolyploids* and originate within a species; those that result from the introduction of a different set into the nucleus as happens in a species cross are known as *allopolyploids*.

made to bloom simultaneously, so providing opportunity for cross-pollination.

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GLOSSARY

ADSORPTION: condensation, in the form of a film, of molecules of a gas or of a dissolved or suspended substance upon the surface of a solid.

ALKALINE: applied to soluble substances which neutralize acids and turn litmus blue; opposite of acidic.

AMMONIFICATION: the name given to changes that take place in the soil when the complex proteins of plant and animal bodies are decomposed by micro-organisms giving rise to compounds of ammonium.

ANEMOPHILOUS: air-loving. Applied to pollen carried by air currents.

ANTIBIOTICS: the name given to active substances produced by living organisms that act antagonistically upon the growth and activity of other organisms. Some antibiotic substances are formed by only a few specific organisms, others by many different organisms under proper conditions of nutrition. Some organisms produce only one type of antibiotic substance, others form two or even more, chemically and biologically different substances. Some antibiotics are highly toxic to animals; others are non-toxic or of limited toxicity. Owing to its great therapeutic value most detailed information is available at present concerning *penicillin*, the antibiotic substance produced by *Penicillium notatum*, a soil fungus.

AUXINS: plant hormones. Substances promoting and directing

the growth of plants, analogous in some ways to the hormones of animal physiology.

Two growth-directing substances have been identified in Flowering Plants, called *auxin A* and *auxin B*. That commonly produced by fungi is called *heteroauxin* and has a very different chemical constitution from the two *auxins*, although producing similar physiological effects.

BIOLOGICAL CYCLE: a series of changes directed by the biological activities of various organisms that can be thus represented diagrammatically (see Nitrogen-cycle).

CALCIUM CARBONATE: $CaCO_3$. Occurs naturally as limestone, marble, and also as *chalk*, formed from the shells of minute marine organisms. The pure crystalline form occurs in nature as *calcite*.

CAMBIUM: a meristematic (q.v.) layer of plant tissue.

CARBOHYDRATE: a chemical substance composed of carbon, hydrogen and oxygen, the two last-named elements being present always in the ratio of 2:1 as in water, H_2O.

CARBON MONOXIDE: CO. An odourless invisible gas. Poisonous, owing to the fact that it combines with the red pigment of the blood, haemoglobin, to form *bright* red carboxyhaemoglobin, thus making the blood incapable of carrying oxygen. Formed during the incomplete combustion of coke, coal, charcoal, etc., at high temperatures. Burns with a blue flame to form carbon dioxide.

CATALYST: a substance which alters the velocity of a chemical reaction but is itself unchanged at the end of the reaction. The use of catalysts finds very wide applications in chemical industry.

CHIMAERA: in the literal sense, a fabulous monster. Used to describe certain kinds of composite plants, the tissues of which are of diverse genetical constitution.

Periclinal chimaeras are those having the dissimilar tissues arranged in a series of skins over a central core; *sectorial*

chimaeras are those which arise from a growing tip in which the dissimilar tissues are arranged in a side-by-side pattern.

CHROMOSOME: thread-like or rod-like structures in the nucleus that become clearly defined during nuclear division. The number of chromosomes is constant for any one organism.

CLONE: plants originating from a common source by vegetative propagation are described botanically as belonging to the same *clone*.

CHLOROPLAST: the green pigment, chlorophyll, occurs in the cells composing the green parts of plants as small green granules or chloroplasts. Each is a sponge-like plastid containing chlorophyll in the meshes.

COAL GAS: fuel gas manufactured by the destructive distillation of coal in closed iron retorts. Composition by volume (average values) hydrogen, H, 50 per cent, methane, CH_4, 30 per cent, carbon monoxide, CO, 8 per cent, other hydrocarbons, 4 per cent, nitrogen, carbon dioxide and oxygen, 8 per cent.

COLCHICINE: a toxic substance extracted from tissues of the Meadow Saffron, *Colchicum autumnale*.

CONIFER: a member of Coniferae, the largest and most important group of Gymnosperms. Most are evergreen trees of erect habit, and grow in dense forests, forming a characteristic feature of the vegetation in many parts of the world.

CUTINIZED: applied to the walls of plant cells impregnated with cutin, a substance rendering them impervious to water. Found especially in the outer walls of the epidermal cells as a waterproof layer or cuticle.

DENITRIFICATION: the process by which combined nitrogen is set free as molecular nitrogen gas by the action of denitrifying bacteria. (See Nitrogen-cycle.)

DICOTYLEDON: a member of the group of Flowering Plants, seedlings of which have two seed leaves or cotyledons.

DIFFUSION GRADIENT: molecules or ions of a substance in solution move freely through the solvent, the solution becoming uniform in concentration. A diffusion gradient is produced as a result of movement taking place from a region of higher concentration towards one of lower concentration.

DIPLOID: having the double set of chromosomes normal for the species.

DORMANCY: a condition of living organisms in which most of the vital activities cease or are slowed down to a very low level.

EGG-CELL: the female sex-cell or gamete that after fertilization grows into a new individual.

ESTER: organic compounds corresponding to salts, the hydrogen of the organic acid being replaced by an organic group. For example, from acetic acid, $CH_3 \cdot COO \cdot H$, is derived the ethyl ester $CH_3 \cdot COO \cdot C_2H_5$, known as ethyl acetate, corresponding to sodium acetate, $CH_3 \cdot COO \cdot Na$.

ETHYLENE: C_2H_4, a hydrocarbon. A colourless inflammable gas with a sweetish smell. (One of the 'other hydrocarbons' in coal gas, q.v.)

FLUORINE: F, an element. Atomic weight 19·00. Pale greenish-yellow gas with a choking smell; extremely reactive.

Occurs combined as fluorspar, a natural form of calcium fluoride, and as cryolite, natural sodium aluminium fluoride, used in the manufacture of aluminium.

FUNGUS-ROOT: see *Mycorrhiza*.

GAMETE: a sex-cell. Sexual reproduction in organisms involves the production of sex cells or gametes, from fusion of which is produced a new individual. Gametes may be similar as in the lower plants, or differentiated into male and female, differing physiologically and usually also in their morphological characters.

GENES: the bearers of the hereditary traits of any plant or animal; carried in the chromosomes.

GRAFT HYBRID: a composite plant produced by the fusion of a nucleus of a *scion* consisting of one kind of plant with a nucleus of the *stock* of another on which it has been grafted. A true graft hybrid thus always originates from a nuclear fusion and the resulting individual shows characters carried by both stock and scion.

GRAM-POSITIVE: bacteria that stain with the dye gentian violet when used in accordance with the technique devised by Gram are said to be Gram-positive.

GROWTH HORMONE: see auxin.

HAPLOID: having the number of chromosomes normally present in the gametes before their fusion, when the full (diploid) number characteristic for the species, is restored.

HORMONES: specific substances produced by the endocrine—ductless—glands of the body, regulating many different functions. Each is an organic compound of a very complex nature, e.g. *insulin*, secreted by the pancreas, maintains the concentration of sugar in the blood at a constant level.

HUMUS: the complex mixture of dark-coloured organic substances formed during the decomposition of plant and animal residues in nature, usually in soils, peat bogs or water basins, also in composts. It plays an important part in the formation of most soils and exerts a variety of chemical, physical, and biochemical influences upon the soil, making it a favourable substrate for plant growth. The origin and character of the soil humus are connected by many invisible ties with the activities of the organisms that have their home in it.

HYBRID: an individual resulting from sexual reproduction between members of different races or varieties, species, or even genera of plants or animals.

HYDROCARBON: a chemical compound consisting of hydrogen and carbon only.

HYDROGENATED: to hydrogenate is to subject a substance to the chemical action of, or cause it to combine with, hydrogen.

HYDROPONICS: 'soil-less culture'. The cultivation of plants by the use of solutions of those mineral salts which a plant normally extracts from the soil.

The plants can be grown in suitable solutions of these salts in *water culture* or planted in clean sand or other suitable material irrigated with the same solutions as *sand cultures*.

INCOMPATIBILITY: the kind of sterility observed in certain groups of plants in which there is no defect in the reproductive organs yet they are fertile only with pollen from certain other varieties with which they are said to be compatible. Some plants cannot be effectively pollinated by their own pollen; they are self-incompatible.

INDOLE: a natural substance found in plants, e.g. in essential oil of Jasmine. Chemically, it is defined as a substance containing a complex nucleus made up of a benzene ring and a pyrole ring.

ISOTOPES: varieties of an element, identical in chemical properties but differing in atomic weight. Many elements are mixtures of isotopes: e.g. bromine, atomic weight 79·916 is a mixture of two isotopes of atomic weights 79 and 81.

LICHEN: a composite plant formed by the close association of cells of an alga, one of the simplest green plants, with mycelium of a fungus.

MEIOSIS: in sexual reproduction the number of chromosomes present in the cell nucleus is doubled at fertilization owing to the fusion of two sex-cells or gametes. Return to the condition normal for the species concerned is due to a special and elaborate *reduction* process before the formation of the next generation of gametes.

This reduction process occurs during a phase in the life history known as *meiosis* involving two closely associated nuclear divisions.

MENDELIAN CHARACTER: an inherited character behaving according to the Mendelian laws of inheritance.

MERISTEM: a plant tissue composed of living cells, all of which are capable of division.

MITOSIS: the name given to the elaborate process during which the cell nucleus divides into two precisely similar parts as occurs during vegetative growth.

MONOCARPIC: in plants, the production of fruit and seed only once in the lifetime of the individual.

MUTATION: a new variety of any given species formed by the sudden appearance of some new character or characters not to be explained by any of the known laws of heredity.

MYCORRHIZA: literally, fungus-root. The name given by Frank, a German botanist, in 1885 to those roots of trees that are composite organs, consisting in part of root tissues and in part of fungus mycelium, associated together to form an organ of constant and definite structure. The use of the name was subsequently extended to all roots showing a regular association with fungus mycelium.

NITRIFICATION: the conversion of ammonium salts to nitrates that takes place in the soil as a result of the vital activities and unusual food preferences of two specialized kinds of bacteria. One of these, *Nitrosomonas*, consumes compounds of ammonium and produces *nitrites* as an end-product; the other, *Nitrobacter*, uses nitrites as a source of nutrient and converts them into *nitrates*.

NITROGEN-CYCLE: Nitrogen, in the form of complex organic compounds, constitutes an essential part of the fabric composing the bodies of plants and animals. After death, and in animals also during life as various excretions, these nitrogenous materials are returned to the soil, where, after

passing through certain phases of vital and chemical activity, they become converted to nitrates.

When absorbed in this simple inorganic form by the roots of green plants, the nitrogen is once more built up into the complex substances of the plant and animal body.

During this complicated cycle of events, however, there may be some loss of nitrogen by the action of denitrifying bacteria, as a result of which nitrogen is released from combination and returned to the air as nitrogen gas unavailable to ordinary plants.

NITROGEN-FIXATION: the utilization of the free nitrogen of the air by certain organisms in their nutritive processes to build up nitrogen-containing compounds. The cases best known are the free-living soil bacteria *Clostridium* and *Azotobacter*, and the nodule bacteria, species of *Pseudomonas*, responsible for forming the root nodules of legumes and certain other plants (see Nodules). Some nitrogen is also 'fixed' by the action of atmospheric electricity; also artificially on an industrial scale.

NODULES: used in reference to the nodular structures formed on the roots of legumes and other plants as a result of invasion of the root tissues by certain soil bacteria that possess the property of using nitrogen gas during nutrition, thus 'fixing' it in the organic materials of which their bodies are composed. (It should be noted that some nodule bacteria lack the ability to fix nitrogen although their entry into the root provokes formation of nodules.

NUCLEIC ACID: a protein substance found in relatively large amounts in the nuclei of plant and animal cells (see Protein).

NUCLEUS: a specialized structure found in nearly all living plant and animal cells.

PARASITE: an organism living in or upon the body of another, using the body substance of the latter while still alive wholly or partly for its own nutrition.

PARTHENOGENESIS: development of a new individual from an egg-cell without fertilization by a male gamete.

PHOTOPERIODISM: the reactions of plants to light in the form of definite lengths and alternations of daylight and darkness; the response to the relative length of day and night. The most obvious effect is on time of flowering. There are 'long day' and 'short day' plants according to the length of daily exposure to light required in order to reach the flowering stage. Some plants are not sensitive to the length of day to which they are exposed.

PHOTOSYNTHESIS: the function in green plants by which the elements of carbon dioxide and water are combined to form carbon compounds. The energy used in this process is derived from certain wave lengths of light intercepted by the pigment chlorophyll present in the green parts of plants.

PLASTID: a specialized particle or granule of protoplasm in a plant cell concerned with individual activities.

POLYPLOID: an individual having more than the two sets of chromosomes normal for the species.

PROTEIN: a complex nitrogenous substance formed in the bodies of plants and animals. The chemical basis of the living material, protoplasm consists of a number of proteins. The albumin in white of egg is a typical protein.

RESPIRATION: the breathing process of plants and animals. Chemically, a decomposition process during which complex organic materials are broken down to form simpler bodies, so releasing the energy used in their construction.

SAPROPHYTE: an organism living upon the *dead* tissues or waste materials of another, i.e. one living upon dead organic material.

SELENIUM: Se. An element; atomic weight 78·96. Non-metal, resembling sulphur in chemical properties. Occurs in nature as selenites of the metals together with sulphides.

SELF STERILITY: the name given to a condition known among fruit trees and other plants in which effective fertilization of the egg-cell cannot be effected by the pollen of the same flower.

SEXUAL REPRODUCTION: the union of sex-cells or gametes to give rise to a new individual.

STRATIFICATION: the name given by botanists to methods by which the germination of certain seeds is artificially regulated and controlled.

SYMBIOSIS: a term first used by the botanist de Bary in 1879 to describe the *living together of dissimilar organisms* without reference to the relations existing between them. In modern usage, the term usually implies a mutualistic or reciprocal relationship benefiting both partners.

TETRAPLOID: having twice the number of chromosomes present in the diploid individual of the same species.

TRACE ELEMENT: in addition to the major essential elements required in nutrition, it has been discovered that plants require minute quantities or *traces* of others, e.g. *boron, zinc, copper*, etc., in order to grow normally. These have been called *minor elements* or *trace elements*. They must not be confused with *tracer elements*.

TRIPLOID: in a hybrid between diploid and tetraploid individuals the gamete from the former contributes *one* set of chromosomes, that from the latter *two* sets, thus making three sets in all, the number characteristic of a *triploid* individual. (See diploid and tetraploid.)

TRYPTOPHANE: a chemical constituent of proteins formed when these are digested with the enzyme, *trypsin*.

ULTRA-MICROSCOPIC: too small in size to be seen with the ordinary compound microscope.

UREA: carbamide, $CO(NH_2)_2$. A white crystalline organic compound. Occurs in the urine of animals. Of interest as

the first organic compound to be prepared artificially in the laboratory.

VALENCY: the combining power of an atom; the number of hydrogen atoms with which an atom will combine with or replace; e.g. oxygen in water, H_2O, is divalent.

VERNALIZATION: the reaction of plants to temperature in the very early stages of germination of the seed. The term is specially associated with the work of Lysenko and his associates in Russia who devised the method of chilling the slightly sprouted grains of cereals and other seeds. By this method seed of the so-called 'winter wheats' can be sown at any convenient time in spring and the plants will come to maturity at the normal season. Unvernalized seed of winter wheat, sown in spring, does not flower or fruit in the same season.

VIRUS DISEASE: infectious disease caused by a *virus*, the infective agent in which can pass through a filter capable of stopping the smallest known micro-organism. Virus diseases of plants are usually spread by sucking insects such as aphides that feed upon the sap of affected plants, each such agent being known as a *vector*. Among virus diseases of animals are smallpox and measles.

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